JOURNAL OF AGRICULTURAL RESEARCH

VOL. X WASHINGTON, D. C., AUGUST 27, 1917 No. 9

BIOLOGIC FORMS OF PUCCINIA GRAMINIS ON CEREALS AND GRASSES[1]

By E. C. STAKMAN, *Head of the Section of Plant Pathology, Division of Plant Pathology and Botany, Department of Agriculture, University of Minnesota,* and F. J. PIEMEISEL, *Scientific Assistant, Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture*

COOPERATIVE INVESTIGATIONS BETWEEN THE AGRICULTURAL EXPERIMENT STATION OF THE UNIVERSITY OF MINNESOTA AND THE BUREAU OF PLANT INDUSTRY OF THE UNITED STATES DEPARTMENT OF AGRICULTURE

INTRODUCTION

The question as to which biologic forms of *Puccinia graminis* Pers. occur on wild grasses is important. Considerable work has been done on the biologic forms of stemrust on the common cultivated cereal grasses, and some has also been done on the relation of the rust on wild grasses to that on cereals. However, on account of the scientific and practical importance of obtaining further information on the identity of the biologic forms of *P. graminis* on wild grasses and the importance of determining the degree of plasticity of these forms when subjected to changed environments, preliminary work on the problem was begun at the Agricultural Experiment Station of the University of Minnesota in the spring of 1913. Since 1915 the work has been done in cooperation with the Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture. The cooperative arrangement has made possible more extensive work and has also given it broader scope.

The object of the work was to determine first the wild hosts for the various biologic forms of *P. graminis*. An attempt was made to determine the frequency of association of any given biologic form with a particular host, the possible geographical localization of biologic forms, the possible variation in parasitic capabilities of forms from different hosts and different localities, and the possible relation of the facts obtained to cereal-rust epidemiology. In order to obtain facts of value on the last-named phase of the problem, it was necessary to make observations on the origin of the early spring infections, the relation of barberries (*Berberis* spp.) to the occurrence and behavior of rust, and to

[1] Published, with the approval of the Director, as Paper No. 67 of the Journal Series of the Minnesota Agricultural Experiment Station.

investigate thoroughly the possibility of changing the parasitic tendencies and capabilities of any biologic form by the use of so-called bridging hosts, by confining a form for a long period of time to uncongenial hosts in an attempt to increase the virulence, and by determining the effect of ecological factors on the rust. The results of the studies of the plasticity of biologic forms will be published in a subsequent paper. The present paper deals mainly, therefore, with the identity of the biologic forms on various hosts.

The problem has received considerable attention both in the United States and in foreign countries. Hitchcock and Carleton (15, 16),[1] Carleton (5, 6, 7), Arthur (1, 2), Bolley (3), Bolley and Pritchard (4), Freeman and Johnson (14), Johnson (19), Pritchard (22, 23), Mercer (21), Stakman (24, 25), Stakman and Jensen (26), and Stakman and Piemeisel (27, 28, 29), have done work on various phases of the question in the United States. The taxonomic work of Arthur and the extensive inoculation experiments of Carleton, followed by the work of Freeman and Johnson with the biologic forms on cereals, have especially laid the foundation for further work. In Europe Eriksson (8–11), Eriksson and Henning (12, 13), and Jaczewski (18) have made extensive investigations. The results are well summarized by Klebahn (20). Although the results obtained by these investigators are usually in general agreement, yet there often are differences which indicate clearly the necessity for thoroughgoing work in different regions. A detailed discussion of these results, in so far as they bear directly on the problem under consideration, will be postponed until after the writer's results are given. Two examples, however, may be cited to show the necessity for further work.

Jaczewski (18, p. 353) states that in Russia *Dactylis glomerata* is immune to *P. graminis avenae*, but is infected by *P. graminis secalis*. Eriksson (11, p. 601), on the other hand, found that in Sweden the same grass is susceptible to *P. graminis avenae* and Carleton (6, p. 63) found the same to be true in this country. Carleton (6, p. 54) also reports successful infection with *P. graminis tritici*. Again, Carleton (6, p. 64) gives the following as hosts for *P. graminis avenae:* Oats (*Avena sativa patula*, *A. sativa orientalis*, and *A. sativa nuda*—cultivated varieties), *Dactylis glomerata*, and *Arrhenatherum elatius*. Pritchard (22, p. 181) obtained results indicating that one form of rust infected rye, oats, *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, and *Avena fatua*. Of these, Carleton (6, p. 56–57) found that *Hordeum jubatum* was certainly a host for *P. graminis tritici* and *Agropyron tenerum* probably so, whereas neither was a host for *P. graminis avenae*, facts which have been confirmed by the writers. Moreover, the writers have been unable to infect *Agropyron tenerum* and *Hordeum jubatum* with *P. graminis* from oats,

[1] Reference is made by number to "Literature cited," p. 493–495.

although it is quite probable that *Hordeum jubatum* may be infected very rarely and weakly. Carleton's work was done largely in the southern wheat-growing area of the Mississippi Valley, while Pritchard's was done in North Dakota. This suggests a possible geographical specialization of the stemrust, and the writers therefore attempted to obtain inoculating material from as many different sources as possible.

REGION COVERED BY THE SURVEY

The work reported in this paper was confined mainly to the upper Mississippi Valley, especially Minnesota, North Dakota, South Dakota, northern Iowa, northern Nebraska, northeastern Wyoming, Montana, and part of the Red River Valley of Manitoba, Canada. Preliminary work was also done in a small part of the intermountain area of the Northwest, especially in Washington and Idaho. It would be highly desirable to extend the work over the cereal-producing regions of the entire United States and Canada.

EXPERIMENTAL METHODS

The rusted grasses were collected in the field, kept in separate envelopes, and immediately sent to the Minnesota Experiment Station, where all inoculations were made. Great care was always taken to avoid any mixing of spores on different grasses. When collecting, the hands were thoroughly washed after each species of grass was handled; or, when this was impossible, the grass was grasped with the collecting envelope as a protection against contaminating the hands with spores.

Inoculations were usually made with comparatively fresh uredinio-spores, although it was sometimes necessary to use rather old material. Inoculations were made in a few cases a month or longer after the grasses had been collected. The viability of the spores had sometimes been impaired somewhat, but at other times they germinated readily. In making the inoculations every precaution was taken to maintain aseptic conditions, and the writers are confident that erroneous conclusions were not drawn as a result of accidental infection when working with different strains. Usually one person worked with only one strain during the day, although it was sometimes necessary to work with more. The plants to be inoculated were grown in a greenhouse compartment where no rust was kept. They were grown under cages made of two layers of a fine-mesh muslin with a dead-air space between the two.

The inoculations on cereals were all made on the leaves or sheaths of seedlings. It was found that the results were comparable with those obtained on older plants. The inoculations on grasses were sometimes made on old plants. In general, the best results were obtained on young, vigorously growing plants, although with some grasses the opposite seemed to be true. Although the writers observed no cases of immunity

due to age, the rust was nevertheless often distinctly more virulent on younger or older plants, depending on the peculiarity of the grass.

The plants to be inoculated were moistened either with an atomizer or by rubbing water on with the fingers. The spores were applied with a flat inoculating needle in such a way as not to injure the leaves. After inoculation the plants were placed in pans of water under thoroughly cleaned bell jars, where they were left for 48 hours. They were then removed and placed on ordinary greenhouse benches. During warm weather, when it was necessary to keep the ventilators open much of the time and there was some danger of contamination with wind-borne spores, each strain was kept under a separate muslin cage such as those under which the seedling plants were grown. A cage was not used again for another strain of rust until first thoroughly disinfected with formaldehyde solution.

All necessary precautions were taken to dispose properly of infected material, and the greenhouse benches were drenched frequently with a strong solution of copper sulphate in order to kill any spores which might have fallen from the leaves. Accidental infections were almost entirely avoided, as is shown by the fact that three different biologic forms were kept more than two years, and many others were kept for shorter periods, without any contamination whatever.

Whenever there was any reason to suspect the presence of more than one biologic form on a host as a result of inoculations with urediniospores collected in the field, all available methods were used to isolate these forms before drawing any conclusions. Further attention will be paid to this in a discussion of the specific results obtained.

The following varieties of cereals were used, except where otherwise specified: Oats—Improved Ligowa, Minnesota No. 281; barley—Manchuria, Minnesota No. 105; wheat—Bluestem, Minnesota No. 169; rye—Swedish, Minnesota No. 2. Most of the grass seeds were obtained from the Minnesota Seed Laboratory. A few were obtained from the Montana Seed Laboratory. The seed of the primitive barleys was furnished by Dr. H. V. Harlan, of the Office of Cereal Investigations, United States Department of Agriculture.

RESULTS OF SURVEY

The results of the inoculations made directly from the grasses collected in the field are given in Tables I to XXVII. The direct inoculations constitute only a small part of the work actually done. The various rusts were often cultured in the greenhouse for varying lengths of time, and as many inoculation experiments were made as seemed necessary to establish the identity of the rust completely and to determine whether it was in any way atypical. The results of these inoculations are given, with the discussions of the various biologic forms.

The following biologic forms are discussed in the paper: *Puccinia graminis tritici* Erikss. and Henn.; *P. graminis tritici compacti*, form. nov.; *P. graminis secalis* Erikss. and Henn.; *P. graminis avenae* Erikss. and Henn.; *P. graminis phleipratensis*, comb. nov. = (*P. phleipratensis* Erikss. and Henn.); *P. graminis agrostis* Erikss.

KEY TO TABLES I–XXVII

In Tables I to XXVII "Place" refers to the place of collection, and "Date," to the date on which inoculations were made. The plants inoculated are listed in the same line with place and date and the results are given in the form of a fraction. The denominator indicates the number of leaves inoculated and the numerator the number which developed uredinia. The figures after the semicolon give the number of leaves which were distinctly flecked. The degree of infection is not indicated in the tables, but it is given in the discussions following the tables.

TABLE I.—*Results of inoculations with urediniospores from Agropyron caninum (L.) Beauv.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Hordeum jubatum.*
		1914					
1	St. Paul, Minn.	Aug. 25	2/20	0/20	5/20	4/20	.....
		1915.					
2	.....do.....	Aug. 13	0/46	0/38	30/42	18/21	1/14
3	Mandan, N. Dak.	Sept. 3	19/27	0/5	9/14	5/12;2	.....
4	Emerson, Manitoba, Canada.	Aug. 21	18/18	.....	.....	2/9	.....
5	Winnipeg, Manitoba, Canada.	" 29	20/20	.....	.....	4/22;3	.....

P. graminis tritici compacti is a form recently described by the writers (29) as differing from other biologic forms in its action on most common wheats (*Triticum vulgare* Vill.). There seems to be no valid reason for not considering the timothy rust as a biologic form of *P. graminis*. Further discussion of biologic forms is given after Tables XXVIII to XXXIII.

Reference is sometimes made to strains of a biologic form. This means merely rust with a certain history and does not necessarily indicate that the so-called strain is different from the typical rust of the biologic form in question. For instance, if *P. graminis tritici* had been collected on *Agropyron tenerum* and *Hordeum jubatum* and the rust from each cultured separately in the greenhouse for a number of generations, the two would be known as strains.

It is quite evident from Table I that *Agropyron caninum* is a host for both *P. graminis tritici* and *P. graminis secalis*. It will be observed that in No. 2 only *P. graminis secalis* was obtained from the grass, while in No. 4 and 5 probably only *P. graminis tritici* was present, since the uredinia on rye were very small and were surrounded by dead leaf areas, thus being typical of the uredinia of *P. graminis tritici* on rye. It is possible that both biologic forms were present in No. 3, although the character of infection pointed to the probable presence of *P. graminis tritici* only.

While *Agropyron caninum* is fairly common in the region covered by the survey, it is probably of secondary importance. It is by no means as common as some of the other species of Agropyron, and, although often severely rusted, it can not be considered in the rank of first importance as a means of enabling the rust to spread to cereals.

TABLE II.—*Results of inoculations with urediniospores from Agropyron cristatum*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*
		1915.				
1	St. Paul, Minn.....	Sept. 10	1/13	0/19	25/28	8/16

The results of the one series of inoculations given in Table II show that *Agropyron cristatum* may be infected with both *P. graminis secalis* and *P. graminis tritici*. While only one uredinium developed on wheat, subsequent events show clearly that both forms were present on the grass when collected from the grass garden in which it was growing.

It will be noted in Table II that barley became heavily infected. The rust on the barley proved to be partly *P. graminis tritici* and partly *P. graminis secalis*, mostly the latter. This was shown by a number of successive transfers to barley, wheat, and rye. Both forms were eventually isolated and, after isolation, remained pure; although, if extensive inoculation experiments had not been made, it would have appeared that barley might enable *P. graminis secalis* to infect wheat.

It is quite apparent from Table III that the common form of stem-rust on *Agropyron repens* is *P. graminis secalis*. Of the 307 leaves of wheat which were inoculated only 3 developed uredinia, while not a single one of the various trials on rye was unsuccessful, although in a few cases not all of the inoculated leaves became infected. This is not surprising, however, since many of the inoculations were made during the hottest weather of the summer, when conditions for infection were unfavorable. Rye plants vary considerably in their susceptibility to *P. graminis secalis*, probably on account of their heterozygous character, and this naturally accounts for some of the variability of infection.

TABLE III.—*Results of inoculations with urediniospores from Agropyron repens (L.) Beauv.*

No.	Place.	Time.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron caninum.*	*Agropyron cristatum.*	*Agropyron imbricatum.*	*Agropyron smithii.*	*Agropyron repens.*	*Boutelcua curtipendula.*	*Bromus tectorum.*	*Elymus canadensis.*	*Elymus robustus.*	*Elymus virginicus.*	*Hordeum jubatum.*
		1915.															
1	St. Paul, Minn.	June 15	0/25	0/22; 1	15/15	14/14	.....	9/14	2/6	.....	.....	.....	.....	.....	.....	26/39	.....
2	.....do.....	June 22	0/35	0/42	43/44	31/32	.....	.....	.....	.....	.....	.....	0/22; fl	.....	.....	.....	.....
3	.....do.....	July 9	1/53	0/42	64/67	56/56	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
4	.....do.....	July 14	1/43	0/24	.....	12/19	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
5	.....do.....	July 19	0/25	0/21	27/30	26/27	.....	.....	.....	.....	.....	0/11	3/11	17/17	13/13	7/11	7/8
6	.....do.....	July 21	.....	0/43	45/45	16/16	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
7	Albert Lea, Minn.	July 24	0/22	0/28	42/42	38/38	5/8	.....	.....	7/7	.....	.....	0/7; 4	3/8	12/12	5/8	.....
8	St. Paul, Minn.	July 27	0/41	0/24	25/28	16/23	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
9	Montevideo, Minn.	July 29	0/18	0/11	5/15	4/9	.....	.....	.....	.....	.....	.....	.....	.....	4/7	.....	.....
10	St. Paul, Minn.	Aug. 12	1/46	0/13	30/30	13/22	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	10/16
11	Fargo, N. Dak.	Aug. 23	0/53	0/27	34/34	27/27	.....	.....	.....	.....	34/34	.....	.....	.....	.....	.....	4/4
12	Presque Isle, Me.	...do....	0/34	0/29	24/26	18/18	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		1916.															
13	McIntosh, Iowa.	July 8	0/11	.....	7/8	6/8	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
14	St. Paul, Minn.	July 17	0/11	.....	.....	5/14	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

Many inoculation experiments were made with known strains of *P. graminis secalis* and *P. graminis tritici* on *Agropyron repens*, and the results confirm the conclusions to be drawn from the results given in Table III. The grass is very susceptible to *P. graminis secalis*, while normal infection with *P. graminis tritici* is rare.

It is quite probable that the successful infections on wheat, recorded as No. 3, 4, and 10 (Table III), resulted from chance spores which may have been blown to the *Agropyron repens* before it was taken from the field. It is very doubtful whether uredinia actually were developed on the grass in the field. The reason for suspecting that they were not is that on the wheat leaves which became infected single uredinia were produced, indicating the probable source of infection as being one or, at most, a very few spores. If the infection had resulted from the spores taken from a uredinium, several uredinia would probably have developed on the wheat. There is evidence that *Agropyron repens* does not become infected with *P. graminis tritici* in nature even when opportunities for infection are very favorable. This is shown as a result of inoculations No. 14. The rusted grass plants were growing in a wheat plot which had been thoroughly and frequently sprayed with uredinio spores of *P. graminis tritici* in suspension in water. The wheat plants were all very heavily rusted, and it was supposed that the quack-grass plants might be infected with *P. graminis tritici* also, because they had been inoculated in the same way, but it will be seen by reference to Table III that such was not the case. Only *P. graminis secalis* occurred on the quack-grass plants.

Agropyron repens is very commonly and very heavily rusted with *P. graminis secalis*. It is often among the first of the grasses to become rusted in the spring. Severe epidemics may develop before other grasses become even moderately rusted.

It is quite apparent from Table IV that *Agropyron smithii* may be affected with both *P. graminis tritici* and *P. graminis secalis*. Artificial inoculations show that both can attack the grass about equally well, especially when young seedlings are inoculated. It is interesting to note that in No. 5 nearly every leaf of wheat, rye, and barley became infected. This might very easily at first glance indicate the occurrence of a single biologic form capable of attacking all three of these cereals. The original rust on the grass, however, was unquestionably a mixture of *P. graminis tritici* and *P. graminis secalis*. This is shown clearly in diagram 1. The rust on rye was transferred to rye or barley 14 successive times during a period of 8 months and wheat was inoculated 8 times, but no uredinia developed on any one of the 107 inoculated leaves. Both rye and barley, on the other hand, were easily infected, showing that the rust originally developed on rye was *P. graminis secalis*.

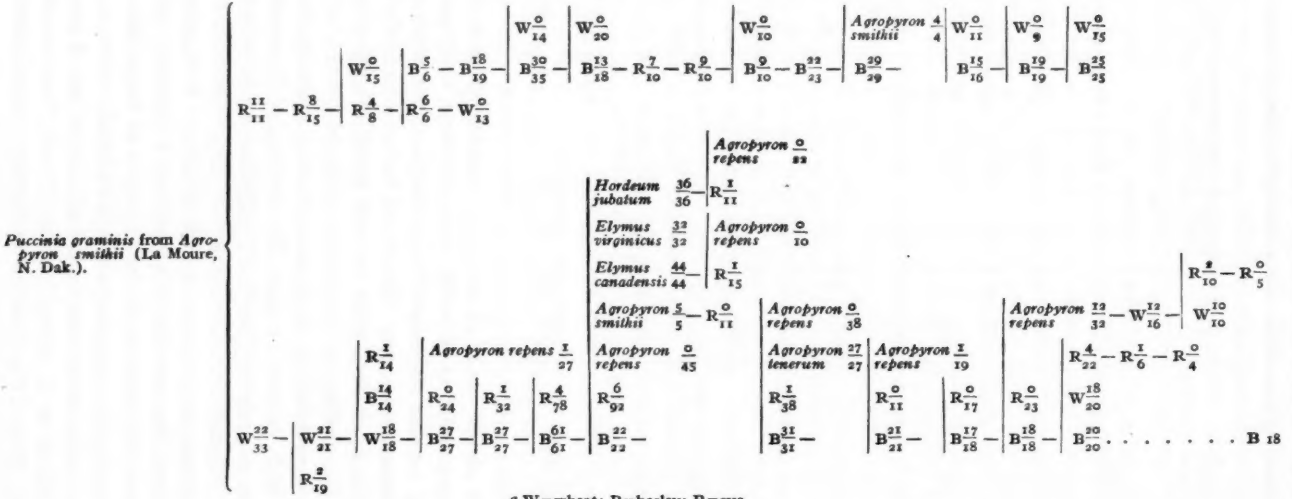
TABLE IV.—*Results of inoculations with urediniospores from Agropyron smithii Rydb.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron smithii.*	*Agropyron repens.*
		1914						
1	St. Paul, Minn.	Aug. 26	5/20	0/20	7/20	15/20	.....	.....
		1915						
2	.....do.....	Aug. 5	0/57	0/35	49/49	25/26	.....	.....
3	.....do.....	Aug. 13	3/21	0/14	6/8	6/10	2/5	.....
4	Mandan, N. Dak.	Aug. 27	10/10	0/10	12/13	1/13	5/6	0/20
5	La Moure, N. Dak.	Aug. 26	22/23	0/12	9/13	11/11	.....	.....
		1916						
6	Denver, Colo.	Aug. 5	0/20	.....	.....	0/14	.....	.....
7	Devils Lake, N. Dak.	Sept. 19	1/13	.....	.....	13/16	.....	.....
8	Minot, N. Dak.	Sept. 20	22/22	0/21	.....	0/20;3	.....	.....
9	Glasgow, Mont.	Sept. 20	33/34	.....	.....	3/30;1	.....	.....
10	Havre, Mont.	Sept. 20	14/15	.....	.....	0/17;1	.....	.....
11	Williston, N. Dak.	Sept. 22	20/20	.....	12/13	0/18;1	.....	.....
12	Newcastle, Wyo.	Oct. 12	0/19	.....	.....	0/15;2	.....	.....

From the rusted wheat 18 successive transfers were made during a period of 10 months, 17 of which were to barley Only about one-half of the total number are shown in the diagram; the other results were similar to those shown here. Wheat and barley were easily and heavily infected when inoculated, while rye and *Agropyron repens* were weakly infected. The uredinia of *P. graminis tritici* on rye are very small and are usually surrounded by dead areas, thus being easily distinguishable from those of *P. graminis secalis*. The uredinia of *P. graminis tritici* on *A. repens* are as a rule very small, although there seems to be considerable variation. Whether this is on account of the condition of the seedlings or the conditions for infection is still doubtful. It is quite clear from the behavior of the rust that this form was *P. graminis tritici*.

The reason why only 12 of the 16 leaves of wheat inoculated with the rust from *Agropyron repens* developed uredinia, whereas 100 per cent of the leaves became infected in the subsequent set of inoculations, is that the uredinia on *A. repens* were very small, thus necessitating light inoculation. Four of the wheat leaves therefore escaped infection. Those

DIAGRAM 1.—Results of successive transfers of rust from wheat and rye in No. 5, Table IV.[a]



[a] W=wheat; B=barley; R=rye.

leaves which became infected, however, developed large uredinia, thus furnishing ample material for the next inoculations.

It is especially interesting to notice the results of the successive transfers of the wheat rust from rye to rye. The rust develops very poorly, and, since the amount of the inoculating material as a rule decreases with each successive transfer, the rust is finally lost. It is also interesting to note that barley, a host for both forms of rust, did not change the parasitic capabilities of either.

The diagram shows, then, that on the original *Agropyron smithii* both *P. graminis tritici* and *P. graminis secalis* were present. For this reason successful infection resulted on wheat, rye, and barley. But when transfers were made from rye to barley, rye, and wheat, only the first two became infected. When, on the other hand, transfers were made from the rusted wheat, wheat and barley were infected, and rye only occasionally produced small, characteristic uredinia, which are distinguishable from those of *P. graminis secalis* both in appearance and performance. Both rusts easily infected barley and *A. smithii*.

Agropyron smithii is very abundant and is very often rusted. In 1916 it was very heavily rusted throughout the Northwestern States and southern Manitoba, Canada. There has been no difficulty in finding badly rusted plants during the last five years. On account of the fact that the grass is a host for two distinct biologic forms, and possibly a third, it is probably important in stemrust distribution.

TABLE V.—*Results of inoculations with urediniospores from Agropyron spicatum (Pursh.) Rydb.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*
		1916.				
1	Glasgow, Mont.....	Sept. 18	$\frac{13}{14}$	$\frac{0}{12}$	$\frac{12}{16}$	$\frac{2}{14}$; 1

Only one set of inoculations was made with *Agropyron spicatum* from east of the Rocky Mountains, although it was quite badly rusted in most localities visited from Glasgow, Mont., west to the mountains. The rust was ordinary *P. graminis tritici*. *P. graminis* was also collected on the grass west of the mountains, but the spores were not viable when inoculations were made. Unfortunately, therefore, the identity of the biologic form of the rust in that region could not be determined with certainty (Table V).

In every one of the 15 trials recorded in Table IV, some wheat became infected, indicating that *P. graminis tritici* often occurs in many regions on *Agropyron tenerum*. On the other hand, *P. graminis secalis* developed only as a result of inoculations 1, 2, and 7, and some of the uredinia in No. 7 were unquestionably *P. graminis tritici*.

TABLE VI.—*Results of inoculations with urediniospores from Agropyron tenerum Vasey*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron repens.*	*Agropyron caninum.*	*Hordeum jubatum.*
		1914.							
1	St. Paul, Minn.....	Aug. 20	2/20	0/20	5/20	13/20	.....	.....	.....
		1915.							
2	.....do.....	Aug. 12	16/82	0/38	55/61	40/61	.....	.....	12/19
3	Valley City, N.Dak.	Aug. 21	2/10	0/14	11/14	2/11	.....	.....	.....
4	Dickinson, N. Dak.	Aug. 27	1/8	0/14	10/12	.....	16/16	13/13	.....
		1916.							
5	St. Paul, Minn.....	July 17	1/10	.....	5/10	0/25	.....	.....	.....
6	Crookston, Minn....	Aug. 21	12/12	.....	.....	0/9; 2	.....	.....	.....
7	.....do.....	Aug. 21	30/30	.....	.....	7/23	.....	.....	.....
8	Emerson, Manitoba.	Aug. 21	25/25	.....	11/11	3/17	.....	.....	.....
9	Glasgow, Mont.....	Sept. 18	13/19	0/20	.....	0/12; 2	.....	.....	.....
10	Williston, N. Dak..	Sept. 19	.....	0/16	[a]20/20	0/11; 2	.....	.....	.....
11	Havre, Mont.....	Sept. 20	14/14	.....	.....	1/19; 6	.....	.....	.....
12	Minot, N. Dak.....	Sept. 21	.....	0/17	[a]23/23	.....	.....	.....	.....
13	Glasgow, Mont.....	Sept. 22	22/22	.....	.....	0/21; 1	.....	.....	.....
14	.....do.....	Sept. 30	15/21	.....	.....	2/16	.....	.....	.....
15	Newcastle, Wyo....	Oct. 2	8/10	0/23	.....	2/13; 4	.....	.....	.....

[a] *P. graminis tritici;* both transferred readily to wheat, not rye.

Inoculations on *Agropyron tenerum* with known strains of *P. graminis tritici* and *P. graminis secalis* show very clearly that it is very susceptible to both forms, thus confirming the results of the inoculations with rust collected in the field (Table VI).

Agropyron tenerum is almost always rusted, sometimes very severely. In the summer of 1916 especially it was almost universally very heavily rusted in Minnesota, North Dakota, Montana, northeastern Wyoming, northwestern Nebraska, and northern Iowa. The same was also true in the Red River Valley in Manitoba, at least as far north as Winnipeg. In 1915 the grass was severely rusted in Minnesota and North Dakota, and very probably throughout the northern wheat-growing area.

There can be but little question that *Agropyron tenerum* is very instrumental in spreading and possibly also in the overwintering of the wheat stemrust and the rye stemrust. It is especially important because it is a congenial host for at least these two common biologic forms and can also be easily infected by *P. graminis tritici compacti.*

TABLE VII.—*Results of inoculations with urediniospores from Agrostis alba L.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agrostis alba.*	*Phleum pratense.*
		1914.						
1	St. Paul, Minn.....	Oct. 23	0/20	0/24	0/20	1/22	.....	.....
		1915.						
2	Albert Lea, Minn.....	July 24	0/36	0/34	1/42	0/35	.....	.....
3	St. Paul, Minn.....	Aug. 17	0/19	12/21	12/36	1/33	.....	.....
4	.....do.....	Sept. 8	0/27	1/34	3/42	0/33	.....	.....
5	.....do.....	Sept. 10	0/28	9/33	1/20	0/14	.....	.....
		1916.						
6	.....do.....	July 7	0/12	0/23	0/5	1/23	.....	0/20
7	.....do.....	July 17	.....	0/16	1/20	0/10	.....	.....
8	.....do.....	Aug. 14	0/19	6/28	9/16	1/22	.....	.....
9	Hinckley, Minn.....	July 21	0/13	0/20	2/13	0/16	.....	.....
10	Crookston, Minn.....	Aug. 21	.....	0/9	.....	.....	30/30	0/38

The stemrust on *Agrostis alba* looks somewhat like *P. graminis phleipratensis.* It infects the cereals in somewhat the same way, and it was at first thought that possibly the rust was *P. graminis phleipratensis,* especially since the urediniospores are nearly equal in size. However, the rust seemed incapable of infecting timothy, and morphologically it differed enough from *P. graminis phleipratensis* to render any idea of the identity of the two rusts untenable. The rust is no doubt *P. graminis agrostis* Erikss., since it infects barberry readily. It is capable of infecting various grasses and oats, barley, and rye. On the three cereals the infection is very weak and resembles that caused by timothy rust very much. The uredinia were always very distinct, but very small. They were usually about 0.25 mm. in diameter, round or slightly elongate, and were not surrounded by large, dead areas as is so often the case when a biologic form develops slightly on an uncongenial host. From the character of the infection it seems quite improbable that *P. graminis agrostis* infects any of the cereals in the field, except possibly very

occasionally. *A. alba* has, however, been infected by *P. graminis avenae* in the greenhouse, although the writers have not found this form on it in the field. It is possible but not demonstrated, therefore, that it may be important as a host for *P. graminis avenae* (Table VII).

TABLE VIII.—*Results of inoculations with urediniospores from Agrostis exarata Trin.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Secale cereale.*	*Calamagrostis canadensis.*
		1916				
1	Whitefish, Mont.	Sept. 30	0/19	24/24	3/25; 2	14/14

Agrostis exarata was heavily rusted in a number of localities, especially in valleys in western Montana. The rust was evidently *P. graminis avenae.* It has been used in many inoculation experiments in the greenhouse, and, although it apparently is an ordinary strain in most respects, the morphology of the urediniospores is slightly different from that of some of the other strains. No sharp differences in parasitic capabilities have yet been noticed (Table VIII).

TABLE IX.—*Results of inoculations with urediniospores of Agrostis stolonifera Vasey*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agrostis alba.*	*Agrostis stolonifera.*	*Agropyron caninum.*	*Phleum pratense.*
		1914.								
1	St. Paul, Minn.	Aug. 26	0/20	0/20	0/20	0/20	.....	.....	.....	.....
2	.....do.....	Oct. 7	0/8	0/21	2/19	1/19	.....	.....	.....	.....
		1915.								
3	.....do.....	Sept. 17	0/23	2/15	0/22	0/20	.....	.....	.....	0/5
		1916.								
4	.....do.....	Aug. 30	.....	.....	.....	.....	60/60	50/50	7/7	.....
5	.....do.....	Sept. 2	0/20	7/22	.....	2/25	.....	.....	.....	.....

DIAGRAM 2.—Results of inoculations from uredinia produced in No. 4, Table IX.

P. graminis agrostis from *A. stolonifera*:
- *A. stolonifera* 50/50 — Wheat 0/34
- *A. canina* 7/7 — Wheat 0/19
- *A. alba* 60/60 — *Calamagrostis canadensis* 3/45

DIAGRAM 3.—Results of inoculations from uredinia produced on oats and rye in No. 5, Table IX.

P. graminis agrostis from *A. stolonifera*:
- Oats 7/22 — Oats 2/15 — Oats 0/7
- Rye 00/25 — Rye — 0/4

Only the three species of Agrostis (Table IX) were really susceptible to *P. graminis agrostis* from *A. stolonifera*. The cereals were infected in much the same manner as were those inoculated with the rust from *A. alba*. The character of the infection was the same. None of the cereals was a congenial host. The uredinia were all very small, but were not surrounded by much dead leaf tissue. Diagram 3 shows that the rust develops only weakly on oats and rye and does not acquire increased virulence as a result of successive transfers. None of the biologic forms commonly found on cereals was found on *A. stolonifera*, although there is reason to suspect that it can be infected naturally by *P. graminis avenae*, since successful transfers were made in the greenhouse.

RESULTS OF INOCULATIONS WITH UREDINIOSPORES FROM AVENA SATIVA

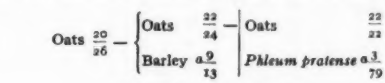
Oats affected with stemrust were collected at various places in Minnesota, North Dakota, and Montana. Inoculations were usually made only on oats, however, and the resulting rust kept as stock cultures. The results are included, therefore, in Table XXXI. Only *P. graminis avenae* was found.

TABLE X.—*Results of inoculations with urediniospores from Anthoxanthum puelli Lecoq. and Lamotte*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*
		1914.				
1	St. Paul, Minn.....	Aug. 23	$\frac{0}{20}$	$\frac{0}{20}$	$\frac{0}{20}$	$\frac{0}{20}$
		1916.				
2	Pullman, Wash.....	Sept. 30	$\frac{0}{19}$	$\frac{20}{26}$	.....	$\frac{0}{18}$

Further inoculations were made with the rust developed on oats. The results are given in diagram 4.

DIAGRAM 4.—Results of inoculations with urediniospores developed on oats recorded in Table X.



a Uredinia extremely minute.

Only a small number of inoculations were made with *P. graminis* from *Anthoxanthum puelli*, but from the results given above, it seems clear that the grass may be a host for *P. graminis avenae*. A number of inoculations with urediniospores of *P. graminis avenae* were made on seedlings of the grass. Some resulted in successful infection, while others did not.

The fact is as yet unexplained. The failure of the inoculations in 1914 was probably due to the fact that the rust on the grass was old.

TABLE XI.—*Results of inoculations with urediniospores from Avena fatua L.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*
		1916.				
1	Williston, N. Dak.	Sept. 18	.....	29/31	1/21; 1	.....
2	Glasgow, Mont.	Sept. 22	3/22	.....	5/24	3/19
3	Pullman, Wash.	Sept. 30	.....	20/21	5/18; 4	.....

Avena fatua can be as easily infected with *P. graminis avenae* as *A. sativa* itself, and is often infected with the stemrust of oats in the field (Table XI). The writers have observed it very often in different localities. Apparently the rust developed on wheat was *P. graminis tritici*. Successful infection can be very easily explained by the fact that the *Avena fatua* plants from which inoculations were made were growing with *Agropyron tenerum* and *A. smithii*, both of which were badly affected with *P. graminis tritici*. The *A. fatua* plants might easily have touched the Agropyrons, thus becoming contaminated with *P. graminis tritici*. The rust developed on barley and rye was undoubtedly *P. graminis avenae*, since it easily transferred to oats.

A. fatua is also a congenial host for the crownrust of oats. The grass was found quite often heavily rusted.

TABLE XII.—*Results of inoculations with urediniospores from Dactylis glomerata L.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Hordeum jubatum.*	*Dactylis glomerata.*	*Agropyron caninum.*	*Agropyron smithii.*	*Phleum pratense.*
		1914.									
1	St. Paul, Minn.	Aug. 22	0/20	11/19	0/20	0/20	.....	.....	.....	.....	.....
		1915.									
2	Ramsey County, Minn.	Aug. 17	0/21	17/17	6/15	1/14	.....	.....	.....	.....	.....
3	.....do.....	Aug. 19	0/28	5/5	3/22	1/19	0/8	12/12	0/16	0/4	.....
		1916.									
4	Ames, Iowa	July 1	.....	0/25	0/15	.....	.....	.....	.....	.....	4/20
5	Long Beach, Cal.	July 8	0/6	0/13	.....	0/8	.....	.....	.....	.....	0/26
6	St. Paul, Minn.	Aug. 24	0/19	26/36	3/26	1/37; 3	.....	.....	.....	.....	.....

Dactylis glomerata may be affected with either *P. graminis avenae* or *P. graminis phleipratensis* in the field (Table XII). It will be noticed that the grass collected at Ames, Iowa, was affected with *P. graminis phleipratensis*. It is quite probable that both forms of rust may occur on the same plants in the field, but both were not found.

TABLE XIII.—*Results of inoculations with urediniospores from Elymus brachystachys Scribn. and Ball.*

Place.	Date.	*Triticum vulgare.*	*Secale cereale.*
	1916.		
Minot, N. Dak.	Sept. 18	19/20	0/12

The rust on *Elymus brachystachys* was very evidently *P. graminis tritici*. From the results obtained with other species of Elymus it is very probable that *E. brachystachys* can be infected with *P. graminis secalis* also, although there is no experimental proof (Table XIII).

TABLE XIV.—*Results of inoculations with urediniospores from Elymus canadensis L.*

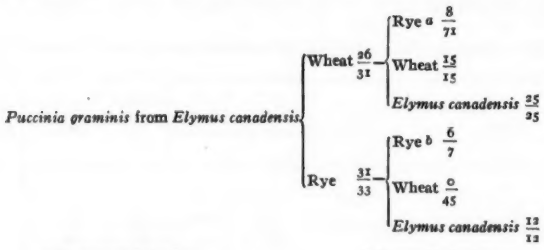
No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron repens.*	*Bromus tectorum.*
		1915.						
1	St. Paul, Minn.	Aug. 19	26/31	.....	33/33	21/33	.....	.....
2	La Moure, N. Dak.	Aug. 26	9/23	0/31	7/13	8/13	.....	.....
3	Minneapolis, Minn.	Nov. 15	0/14	0/20	22/25	12/19	4/25	31/31
		1916.						
4	Brownton, Minn.	Aug. 7	27/27	.....	.....	6/24; 10	.....	.....
5	Devils Lake, N. Dak.	Sept. 15	6/15	0/16	.....	.....	20/20	.....
6	Williston, N. Dak.	Sept. 20	19/19	.....	.....	1/21; 3	.....	.....
7	Minot, N. Dak.	Sept. 21	27/27	0/24	.....	.....	.....	.....
8	Glasgow, Mont.	Sept. 22	24/24	0/23	.....	0/20; 3	.....	.....
9	Pullman, Wash.	Sept. 30	[a] 8/13	.....	.....	0/15; 5	.....	.....

[a] Wheat very distinctly hypersensitive.

Puccinia graminis tritici, *P. graminis tritici compacti*, and *P. graminis secalis* were found on *Elymus canadensis* (Table XIV). The grass is attacked with approximately equal ease by all three forms. In 1915 the wheat and rye forms were commonly found in the upper Mississippi Valley, but in 1916, a year in which there was a very severe wheat-rust epidemic, only *P. graminis tritici* was found, except in No. 4. A considerable amount of rye is grown in the region from which this particular grass material was obtained. It is interesting to note that both forms of rust were present on the rye infected in this experiment. The rust which developed in No. 4 was used in inoculating rye and wheat. On the rye 15 out of 18 leaves became infected and 7 out of 43 wheat leaves developed uredinia.

Elymus canadensis is probably not as important as some of the other grasses in stem-rust epidemiology. It may become very heavily rusted but the rust often develops late in the season, and the grass may almost entirely escape. The habit of growth may account for this fact.

DIAGRAM 5.—Results of inoculations with rust from wheat and rye recorded in No. 1, Table XIV.



[a] Very weak infection. [b] Normal infection.

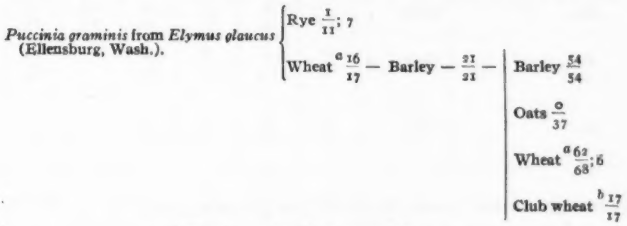
Diagram 5 shows very clearly that both *P. graminis tritici* and *P. graminis secalis* were present on *E. canadensis* in No. 1. It should be remembered, of course, that *P. graminis tritici* can infect rye weakly while *P. graminis secalis* can not infect wheat.

TABLE XV.—*Results of inoculations with urediniospores from Elymus condensatus Presl.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Secale cereale.*
		1916			
1	Ritzville, Wash.	Oct. 3	15/18; 3	0/16	2/14; 7
2	Ellensburg, Wash.	...do.	0/28; fl.	0/18	0/20
3	Pullman, Wash.	Oct. 5	14/17	.....	0/22; 5

Elymus condensatus was almost universally rusted both west of the Rocky Mountains and in Montana, Wyoming, and western Nebraska east of the mountains. Unfortunately no inoculations were made with the rust from east of the mountains, which would very probably have proved to be ordinary *P. graminis tritici*. All of the rust which was used in the inoculations, the results of which are recorded in Table XV, was *P. graminis tritici compacti*.

DIAGRAM 6.—Results of inoculations with urediniospores from *Elymus glaucus* Buckley.


Puccinia graminis from Elymus glaucus (Ellensburg, Wash.).
Rye 1/11; 7
Wheat a 16/17 — Barley — 21/21 —
Barley 54/54
Oats 0/37
Wheat a 62/68; 6
Club wheat b 17/17

[a] Wheat very sharply hypersensitive.
[b] Heavy, normal infection on club wheat.

The character of infection on bluestem wheat, Minnesota 169, shows clearly that the rust was *P. graminis tritici compacti*. The uredinia were always small, and there were large dead spots on the leaves. On barley and club wheat, on the other hand, infection was normal.

TABLE XVI.—*Results of inoculations with urediniospores from Elymus macounii Vasey*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*
		1916				
1	Winnipeg, Manitoba.....	Aug. 24	18/18	.....	.....	4/38
2	Emerson, Manitoba.....	Aug. 22	18/22	0/19	10/10	0/13
3	Havre, Mont.....	Sept. 22	23/23	.....	.....	3/18; 4
4	Ellensburg, Wash.....	Oct. 5	a 11/18; 7	.....	.....	a 0/19; 5

[a] Wheat and rye hypersensitive.

The rust collected at Winnipeg and Emerson, Manitoba, and that collected at Havre, Montana, was all ordinary *P. graminis tritici*, while that collected at Ellensburg, Wash., was *P. graminis tritici compacti*. Both attack the grass very easily and may produce large numbers of spores on it. Although *P. graminis secalis* was not found on *Elymus macounii* in the field, it is quite possible that the grass is susceptible to this form, since the various species of Elymus seem to be quite similar in this respect (Table XVI).

TABLE XVII.—*Results of inoculations with urediniospores from Elymus robustus Scribn. and J. G. Sm.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Elymus canadensis.*	*Elymus robustus.*	*Hordeum jubatum.*
		1915.							
1	St. Paul, Minn.	Aug. 11	1/11	0/33	49/54	33/40	.....	.....	.....
2	.....do.....	Sept. 2	1/21	0/29	32/32	30/30	15/15	13/13	12/12
3	.....do.....	Sept. 8	0/19	0/23	28/36	40/43	.....	13/13	.....
		1916.							
4	.....do.....	July 7	0/21	0/21	15/23	15/21	.....	.....	.....

Puccinia graminis secalis occurred on *Elymus robustus* in all four lots of material from which inoculations were made (Table XVI). A small amount of *P. graminis tritici*, however, was present on the first two lots collected. The grass is about equally susceptible to both the rye and wheat forms of stemrust, this fact being very clearly demonstrated by a great many inoculation experiments. *E. robustus*, like *E. canadensis*, may be severely rusted in the field. In the epidemic of 1916, however, it did not seem to be so universally and severely attacked as some of the species of Agropyron and *Hordeum jubatum*. Just why this was so is difficult to say. Certainly *E. robustus* is quite as susceptible as these other grasses in the greenhouse. However, on account of its habit of growth, conditions for infection may not be so favorable in the field.

TABLE XVIII.—*Results of inoculations with urediniospores from Festuca elatior L.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Phleum pratense.*
		1916.				
1	Ames, Iowa	July 1	.....	.....	2/20	12/30
2	Madison, Wis.[a]	...do.....	.....	0/25	0/18	0/30
3	Bellingham, Wash	Sept. 7	0/27	14/31	2/28; 6	21/21
4	Sheridan, Wyo	Oct. 9	.....	7/26; 4	9/25; 16	.....

[a] Very few spores were viable when inoculations were made.

The rust on *Festuca elatior* was *Puccinia graminis phleipratensis* in both cases where successful infection occurred (Table XVIII). This was easily determined both by the morphology of the spores and the nature of the uredinia developed on oats and barley. The comparatively small

number of leaves of *Phleum pratense* which became infected in No. 1 was probably due to the fact that the grass inoculated had been somewhat injured by thrips. When transfers were made to healthy timothy plants, 15 out of 15 became infected.

TABLE XIX.—*Results of inoculations with urediniospores from Festuca pratensis Huds.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Phleum pratense.*	*Hordeum jubatum.*	*Agropyron repens.*
		1915.							
1	St. Paul, Minn.....	Aug. 10	$\frac{0}{26}$	$\frac{35}{47}$	$\frac{3}{18}$	$\frac{5}{37}$	.....	.....	.....
2	.....do.....	Aug. 10	$\frac{0}{25}$	$\frac{14}{22}$	$\frac{3}{27}$	$\frac{13}{26}$	.....	.....	.....
3	.....do.....	Aug. 16	$\frac{0}{54}$	$\frac{41}{65}$	$\frac{5}{40}$	$\frac{2}{44}$	.....	.....	.....
4	.....do.....	Sept. 2	$\frac{0}{22}$	$\frac{9}{38}$	$\frac{2}{11}$	$\frac{2}{12}$	$\frac{6}{8}$	$\frac{0}{5}$	.....
5	.....do.....	Sept. 2	$\frac{0}{21}$	$\frac{6}{37}$	$\frac{7}{31}$	$\frac{4}{31}$	$\frac{9}{16}$	$\frac{1}{11}$	$\frac{0}{19}$
		1916.							
6	Udell, Iowa.....	July 1	.....	$\frac{3}{67}$	$\frac{7}{31}$	.....	$\frac{45}{45}$	.....	.....
7	St. Paul, Minn.....	Aug. 7	$\frac{0}{19}$	$\frac{15}{33}$	$\frac{3}{22}$; 6	.....	.....	.....	.....
8	Pullman, Wash.....	Sept. 30	.....	.....	$\frac{14}{20}$; 6	.....	$\frac{35}{35}$	.....	.....

The results of the inoculations recorded in Table XIX show that the common rust on *Festuca pratensis* is *P. graminis phleipratensis* and that oats, barley, and rye may be weakly attacked. The rust did not develop well on any of the three, the uredinia always being small.

One set of inoculations was made with *P. graminis* from *Hordeum caespitosum*, collected at Coburg, Mont., on September 22, 1916. The results are given in diagram 7 and show clearly that the rust was *P. graminis tritici*.

DIAGRAM 7.—Results of inoculations with urediniospores from *Hordeum caespitosum* Scribn.

Puccinia graminis from *Hordeum caespitosum* (Coburg, Mont.) { Wheat $\frac{10}{13}$; Rye $\frac{1}{16}$

Three biologic forms of *P. graminis* were found on *Hordeum jubatum*—viz, *P. graminis tritici*, *P. graminis tritici compacti*, and *P. graminis secalis* (Table XX). Both *P. graminis tritici* and *P. graminis secalis* were isolated a number of times from the same lot of grass material. The two forms can be separated easily, as shown by diagram 8. It will be seen by referring to No. 3, Table XX, that all the inoculated leaves of barley,

TABLE XX.—*Results of inoculations with urediniospores from Hordeum jubatum L.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron repens.*	*Agropyron occidentale.*	*Bouteloua curtipendula.*	*Bromus tectorum.*	*Elymus canadensis.*	*Agropyron caninum.*	*Elymus robustus.*	*Elymus virginicus.*	*Hordeum jubatum.*
		1914.													
1	St. Paul, Minn.	June 25	0/24	0/29	24/29	23/23									
2	do	Sept. 8	2/30	4/30	11/30	30/30									
		1915.													
3	do	June 29	8/58		57/57	58/58					81/81		42/42	41/41	
4	do	July 14	1/47	0/56		45/48									
5	Albert Lea, Minn.	July 24	0/44		55/55	28/28									
6	St. Paul, Minn.	July 19	15/25	0/22	41/41	27/32	3/7		0/11	5/15	12/12		17/19	11/11	
7	do	July 21		0/41	48/48	24/24									
8	Jordan, Minn.	July 27	0/36	1/31	36/39	39/45									
9	St. Paul, Minn.	Aug. 5	1/36		25/25	20/20									
10	do	Aug. 5	0/40		24/24	31/35	21/23								
11	do	Aug. 10	14/72		21/38	47/50	35/36								
12	do	Aug. 16	6/42	0/30	25/25	46/49									
13	do	Aug. 16	31/36	0/37	35/35	28/33		3/3				10/10			
14	Lisbon, N. Dak.	Aug. 23	53/53	11/30	38/40	13/38	7/20								
15	do	Aug. 26	30/43	0/27	5/12	5/14									

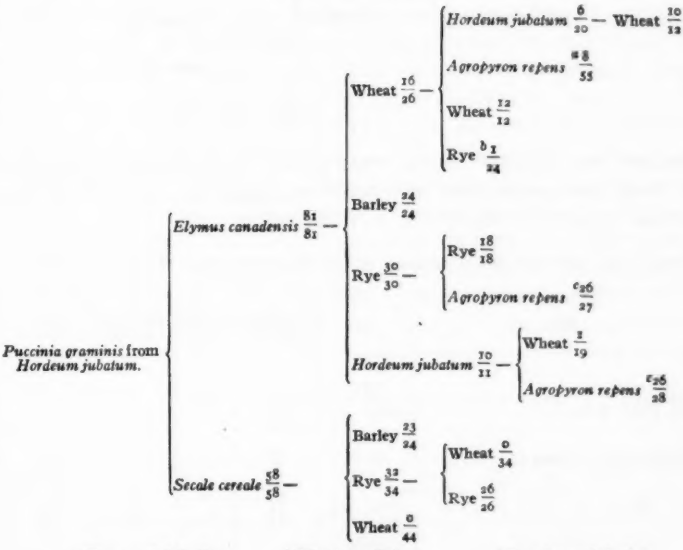
16	Dickinson, N. Dak.	Aug. 27	1/12	0/12	3/10	.....	13/13	.....	.....	.....	.....	.....	.....	.....	.....	.....
17	Minot, N. Dak.	Aug. 30	24/37	2/15	17/17	16/20	9/17	.....	.....	.....	.....	.....	.....	.....	.....	.....
18	Harvey, N. Dak.	Aug. 31	14/23	0/13	11/15	2/15	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
19	Valley City, N. Dak.	Aug. 31	5/26	0/22	13/22	3/28	2/38	.....	.....	.....	.....	.....	.....	.....	.....	.....
20	Jamestown, N. Dak.	Sept. 1	38/41	0/32	7/25	3/26	0/15	.....	.....	.....	.....	.....	.....	.....	.....	.....
21	Moorhead, Minn.	Sept. 1	10/17	0/29	27/27	22/22	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
22	Madison, Wis.	Oct. 6	0/13	.....	.....	6/9; 2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		1916.														
23	Onawa, Iowa.	July 1	.....	.....	12/38	2/11	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
24	McIntire, Iowa.	July 8	0/3	.....	7/11	3/10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
25	Armstrong, Iowa.	July 11	.....	.....	1/23	0/15	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
26	Madison, Wis.	July 11	0/21	.....	.....	10/26	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
27	Hinckley, Minn.	July 31	5/24	.....	.....	4/17; 3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
28	Denver, Colo.	Aug. 5	1/15	.....	.....	0/15	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
29	Watertown, S. Dak.	Aug. 5	12/36	.....	.....	0/32	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
30	Brownton, Minn.	Aug. 7	6/9	.....	.....	0/13; 1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
31	Two Harbors, Minn.	Aug. 14	7/24	.....	.....	24/25	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
32	Grand Rapids, Minn.	Aug. 15	36/38	.....	6/15	6/29; 6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
33	Emerson, Manitoba.	Aug. 21	50/50	.....	.....	2/22	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
34	Hawley, Minn.	Aug. 19	0/40	0/41	2/18	0/34	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

TABLE XX.—*Results of inoculations with urediniospores from Hordeum jubatum L.*—Continued

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron repens.*	*Agropyron occidentale.*	*Bouteloua curtipendula.*	*Bromus tectorum.*	*Elymus canadensis.*	*Agropyron caninum.*	*Elymus robustus.*	*Elymus virginicus.*	*Hordeum jubatum.*
		1916.													
35	Crookston, Minn.	Aug. 21	30/30			6/19									
36	Portage la Prairie, Manitoba	Aug. 24	14/14			2/16									
37	Devils Lake, N. Dak.	Sept. 15	7/17	0/16			25/29								
38	Berwick, N. Dak.	Sept. 15		0/13	18/18		18/37								
39	Churchs Ferry, N. Dak.	Sept. 20	13/14			1/20; 3									
40	Minot, N. Dak.	Sept. 18	9/14	0/15		0/14; 7									
41	Williston, N. Dak.	Sept. 22	17/17	0/17		1/18									
42	Cut Bank, Mont.	Sept. 22	19/19			0/19									
43	Havre, Mont.	Sept. 20	16/16	0/20		5/19; 3									
44	Pullman, Wash.	Oct. 24	16/40; 12		50/53	1/32; 7									9/20
45	Glasgow, Mont.	Sept. 30	15/15			1/13; 2									
46	Sheridan, Wyo.	Oct. 9	10/15			1/22; 1									
47	Newcastle, Wyo.	Oct. 7	12/12			0/7; 2									
48	Crawford, Nebr.	Oct. 9	15/15			2/20; 15									
49	.....do.....	Oct. 12	12/12	0/18		1/11									

rye, and the three species of Elymus became infected, while only a small percentage of the wheat leaves developed uredinia. Barley and the three grasses were known to be congenial hosts for both forms of the stemrust. It was therefore to be expected that each was infected with the two. This proved to be the case, but evidently more of the rye form was present than of the wheat form, as would also be supposed from the results in No. 3. This is shown in the diagram by the fact that not all of the inoculated wheat leaves rusted, while all of the rye leaves did. The weak infection which resulted on *Agropyron repens* and rye from the inoculation with the rust developed on wheat showed that the wheat developed only the wheat form, while the rye very clearly developed only the rye form.

DIAGRAM 8.—Results of inoculations with urediniospores developed on *Elymus canadensis* and *Secale cereale* in No. 3, Table XX.

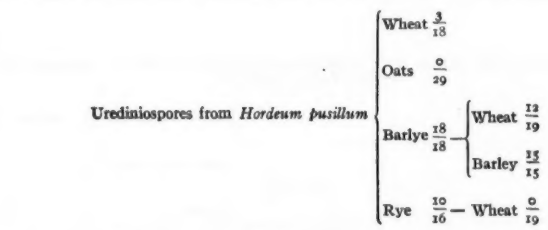


a Very weak infection. b Minute uredinium. c Very heavy infection.

In 1916 very little of the *secalis* form developed. The rust developed on rye in No. 31 was of this form. Except for this one lot of material, however, little or none of the *secalis* form was found during the summer. The uredinia developed on rye in the other trials were small and the flecks sharp, indicating the presence of *P. graminis tritici*. Inoculations from rye to wheat and rye also showed this to be true. *P. graminis tritici compacti* was found on *Hordeum jubatum* only at Pullman, Wash., west of the Rocky Mountains. The rusts east of the mountains were practically the same, although there sometimes appeared to be slight differences in virulence.

Probably no grass is responsible for spreading more wheat stemrust than *Hordeum jubatum*. It rusts early in the season, especially near barberries, and during a season favorable to rust development it becomes almost universally rusted. In amount of rust developed it is approached probably only by *Agropyron repens*, which, however, is host for *P. graminis secalis*, not *P. graminis tritici*. Inconceivably large numbers of urediniospores are developed by these grasses, and when the rusted grass is disturbed on windy days clouds of spores, which are probably carried considerable distances by the wind, can easily be seen.

DIAGRAM 9.—Results of inoculations with urediniospores from *Hordeum pusillum Nutt.*



The rust was collected in the grass garden on University Farm, St. Paul, Minn., and inoculations were made on August 30, 1916. Both the wheat and rye forms were present (see diagram 9).

TABLE XXI.—*Results of inoculations with urediniospores from Hordeum vulgare*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*
		1915.				
1	St. Paul, Minn.	July 17	8/9	.....	.....	.....
2	Ramsey Co., Minn.	...do....	3/6	.....	.....	0/12
3	.....do.....	Oct. 14	29/31	0/16	14/15	1/29
		1916.				
4	Hinckley, Minn.[a]	July 29	2/20	.....	.....	1/15
5	Pine City, Minn.[a]	Aug. 1	4/15	.....	.....	0/10; 5
6	Emerson, Manitoba	Aug. 22	26/31	0/23	10/11	2/15; 4
7	Portage la Prairie, Manitoba[b]	Aug. 24	10/10	.....	.....	2/19
8	Williston, N. Dak.	Sept. 20	18/18	.....	.....	4/15; 3

[a] Greenhouse conditions unfavorable for infection.
[b] Hooded barley.

The work with barley was done particularly to determine whether a special biologic form occurs on barley (Table XXI). Freeman and Johnson (14, p. 19) obtained results which led them to believe this to be the case. The form on barley in their experiments seemed to infect rye and oats more readily than either the wheat stemrust form or the rye form. They therefore named the barley form *P. graminis hordei* F. and J. (14, p. 27). It will be seen from Table XXI that all of the rust collected on barley in the field by the writers was ordinary *P. graminis tritici*. Only two sets of inoculations were made on oats, but successful infection did not occur in either. However, Derr (14, p. 18) successfully infected oats with *P. graminis tritici* taken directly from wheat. Freeman and Johnson (14, p. 20) also succeeded in infecting rye more easily with barley rust than with wheat rust. However, the writers obtained, in a number of sets of inoculations, a greater percentage of infection on rye with *P. graminis tritici* than Freeman and Johnson report having obtained with *P. graminis hordei*. The percentage of leaves of rye which become infected when inoculated with the same strain of *P. graminis tritici* and the degree of infection both vary greatly in different trials.

Further, barley can be infected by all of the common biologic forms of *P. graminis*, and the possibilities for mixed strains on this host are therefore not to be overlooked. It is unquestionably a very congenial host for *P. graminis secalis*, *P. graminis tritici*, and *P. graminis tritici compacti* and can be quite consistently weakly infected by *P. graminis avenae*, *P. graminis agrostis*, and *P. graminis phleipratensis*. It is unquestionably the least specialized of any of the cereals toward *P. graminis*.

It is doubtful, therefore, whether there is a separate biologic form for barley.

TABLE XXII.—*Results of inoculations with urediniospores from Hystrix patula Moench*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Hordeum jubatum.*	*Agropyron caninum.*
		1915.						
1	St. Paul, Minn.	Aug. 10	4/40	0/13	61/68	31/33	.....	.....
2	.....do.....	Sept. 2	4/30	0/29	25/26	21/22	6/6	8/10
3	Ransey County, Minn.	...do.....	.....	.....	12/15	.....	.....	.....

Both *P. graminis tritici* and *P. graminis secalis* may occur on *Hystrix patula* (Table XXII). The *P. graminis secalis*, however, which was isolated from the grass differed somewhat from ordinary strains of this biologic form. The urediniospores are smaller, and the rust is less virulent on the cereals than *P. graminis secalis*. This is especially true of

barley. On this host the rust develops only weakly, while *P. graminis secalis* develops normally. On some of the grasses susceptible to *P. graminis secalis*, however, the *Hystrix patula* strain develops normally. It can very easily infect and develop normally on *Agropyron repens*, *A. tenerum*, *A. caninum*, *Elymus virginicus*, *Hordeum jubatum*, and *Hystrix patula*. While there may be sufficient reason for considering this a separate biologic form, it is probably preferable to consider it only a variant form of *P. graminis secalis* without giving it a new name.

TABLE XXIII.—*Results of inoculations with urediniospores from Koeleria cristata (L.) Pers.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*
		1915				
1	St. Paul, Minn.[a]	May 14	.....	$\frac{5}{6}$	.....	.....
2	.....do.....	May 22	$\frac{0}{17}$	.....	$\frac{0}{18}$	$\frac{0}{7}$
		1916				
3	Manhattan, Kan.[b]	June 5	.....	$\frac{1}{43}$	$\frac{11}{40}$	.....

[a] Grass planted in greenhouse in fall. [b] Material badly dried.

The rust developed in No. 1 (Table XXIII) was undoubtedly *P. graminis avenae*, while that in No. 3 was very probably *P. graminis phleipratensis*. A large number of inoculations were made on the grass with the stemrust of oats, as well as with the other forms of stemrust. The results showed clearly that *Koeleria cristata* is very susceptible to *P. graminis avenae*, *P. graminis agrostis*, and *P. graminis phleipratensis*, but not to *P. graminis secalis*, *P. graminis tritici*, or *P. graminis tritici compacti*.

Panicularia pauciflora was very heavily and commonly rusted in the mountain valleys just west of the Continental Divide in Montana. The rust proved to be ordinary *P. graminis avenae* (diagram 10). The char-

DIAGRAM 10.—Results of inoculations with urediniospores from *Panicularia pauciflora* (Presl.) Kuntze.

P. graminis from *Panicularia pauciflora* —

- Wheat $\frac{0}{16}$
- Rye $\frac{0}{17}$
- Oats $\frac{27}{36}$
- *Phleum pratense* $\frac{0}{27}$
- *Agrostis stolonifera* $\frac{0}{24}$

- Rye [a] $\frac{3}{14}$; 2
- Barley [a] $\frac{12}{14}$; 2 — Barley $\frac{0}{24}$
- Oats $\frac{14}{21}$ — Oats $\frac{21}{24}$ — Oats $\frac{54}{54}$ — Oats $\frac{13}{13}$ . . . [b] Oats $\frac{40}{51}$
- *Dactylis glomerata* $\frac{7}{7}$ — *Phleum pratense* [a] $\frac{7}{35}$ — *Phleum pratense* $\frac{0}{8}$
- *Agrostis stolonifera* $\frac{5}{10}$
- *Calamagrostis canadensis* $\frac{12}{15}$

[a] Minute uredinia. [b] Dots indicate that a number of intervening transfers were made.

acter of infection on the cereals and grasses was the same as that produced by the other strains of *P. graminis avenae* which were tried. The rust developed normally on oats and *Dactylis glomerata*, nearly normally on *Calamagrostis canadensis*, and but very imperfectly on barley, rye, and *Phleum pratense*.

TABLE XXIV.—*Results of inoculations with urediniospores from Phleum pratense L.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agrostis alba.*	*Dactylis glomerata.*	*Phleum pratense.*
		1915.							
1	St. Paul, Minn....	Aug. 17	0/44	30/35	18/46	2/45	.....	.....	30/30
2	.....do.....	Aug. 26	0/44	7/21	9/21	2/26	.....	14/15	2/2
3	.....do.....	Aug. 26	0/38	8/34	4/27	2/36	.....	10/10	9/9
4	.....do.....	Sept. 4	0/31	8/27	2/29	0/17	.....	.....	.....
		1916.							
5	Denver, Colo.....	Mar. 16	.....	.....	.....	.....	.....	.....	25/25
6	.....do.....	Mar. 30	.....	.....	.....	.....	0/9	.....	.....
7	Madison, Wis.....	May 3	.....	.....	1/77	.....	.....	.....	.....
8	Seward, Nebr.....	June 2	.....	.....	9/39	.....	.....	.....	.....
9	Denver, Colo.....	June 20	.....	0/18	24/70	1/15	.....	.....	25/25
10	Worthington, Minn	July 2	.....	.....	0/19	.....	.....	.....	.....
11	Ames, Iowa.....	July 3	.....	.....	9/28	.....	.....	.....	.....
12	Centerville, Iowa..	July 3	.....	.....	10/27	.....	.....	.....	.....
13	Carroll, Iowa.....	July 3	.....	.....	10/40	.....	.....	.....	.....
14	Armstrong, Iowa..	July 11	.....	.....	0/20	.....	.....	.....	.....
15	Long Beach, Cal..	July 11	.....	1/27	0/32	.....	.....	.....	.....
16	Castlewood, S. Dak	Aug. 5	.....	.....	0/17	.....	.....	.....	.....
17	Brookings, S. Dak.	Aug. 5	.....	.....	0/46	.....	.....	.....	4/14
18	Grand Rapids Minn.....	Aug. 15	.....	.....	9/48	.....	.....	.....	15/15
19	Hawley, Minn.....	Aug. 19	.....	.....	0/33	.....	.....	.....	1/15
20	Emerson, Manitoba	Aug. 21	.....	.....	10/37	.....	.....	.....	40/40

TABLE XXIV.—*Results of inoculations with urediniospores from Phleum pratense L.*—Continued

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agrostis alba.*	*Dactylis glomerata.*	*Phleum pratense.*
21	Portage la Prairie, Manitoba	1916. Aug. 23	.....	.....	10/43	.....	.....	.....	14/14
22	Winnipeg, Manitoba	Aug. 23	.....	.....	2/18	.....	.....	.....	18/18
23	Whitefish, Mont	Sept. 30	.....	.....	4/16; 10	.....	.....	.....	.....
24	Ponderay, Idaho	Sept. 30	.....	.....	12/16; 3	.....	.....	.....	.....
25	Pullman, Wash	Sept. 30	.....	.....	7/13; 3	.....	.....	.....	21/21
26	Ellensburg, Wash	Oct. 3	.....	.....	18/31; 11	.....	.....	.....	.....
27	Sheridan, Wyo	Oct. 7	.....	.....	6/15; 8	.....	.....	.....	.....
28	Newcastle, Wyo	Oct. 7	.....	.....	7/14; 5	.....	.....	.....	.....
29	Crawford, Nebr	Oct. 9	.....	.....	10/44; 13	1/1	.....	.....	.....

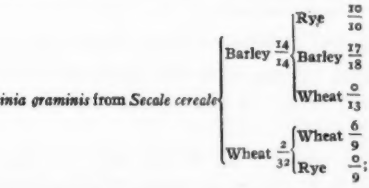
The work with timothy rust had two main objects: (1) To determine whether *Puccinia graminis phleipratensis* varied greatly in different regions, and (2) to ascertain whether the rust could be easily changed. The reason for the investigation was the fact that, whereas previous investigators were unable to infect barley with the rust, Stakman and Jensen (26) found no particular difficulty in doing so, thus suggesting either different strains of the rust in nature, or an ability of the rust to change rapidly. The attempts to increase the virulence of the rust will be discussed in a subsequent paper; the results of the direct inoculations are given in Table XXIV. There was little if any real difference between strains. The rust failed to infect barley in only a few cases. These failures, however, are not surprising, since conditions varied considerably in the different trials. Variable results are often obtained when the same strain of rust is used. It will be noticed that successful infection did not occur to any extent in No. 14, 15, 16, and 17. The reason for this is very probably the fact that the weather was extremely hot during this period. The subsequent inoculations, with one exception, were successful. The percentages of successful infection were especially high in late September and early October, a period during which weather conditions were ideal for rust development in the greenhouse. All rusts developed unusually well during this period, while during the extremely hot weather in July and early August none developed very well.

TABLE XXV.—*Results of inoculations with urediniospores from Secale cereale L.*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Elymus virginicus.*	*Bromus tectorum.*
		1914.						
1	St. Paul, Minn.	June 9	0/22	0/19	13/20	16/18	.....	.....
2	.....do.....	June 16	0/20	0/27	12/17	17/18	.....	.....
3	.....do.....	June 25	0/10	.....	.....	.....	.....	.....
		1915.						
4	Ramsey Co., Minn.	June 17	4/21	1/41	42/44	11/12	35/40	.....
5	.....do.....	June 22	1/35	[a] 2/43	48/48	31/34	12/12	0/23
		1916.						
6	Portage la Prairie, Manitoba.	Aug. 24	2/32	.....	14/14	.....	.....	.....

[a] Minute uredinia.

DIAGRAM 11.—Results of inoculations with rust developed in No. 6, Table XXV.

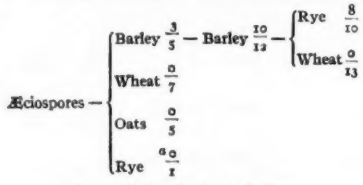


Rye is usually affected with *P. graminis secalis* in the field. It will be noticed that the rust infects barley very readily and can infect oats only occasionally and with difficulty. The uredinia on oats were all very small. *P. graminis tritici* may also occur rarely on rye. The fact that the wheat stemrust and not the rye stemrust infected wheat in No. 6 in Table XXV is shown in diagram 11. The rust on barley was all the rye form, since it could not infect wheat. The rust on the wheat, however, was clearly *P. graminis tritici*, since it infected wheat but produced only two flecks on rye. The very limited infection of rye by wheat stemrust in the field is probably of little practical consequence.

The inoculations reported in diagram 12 were made with æciospores developed on *Berberis vulgaris* as a result of inoculations with teliospore material which was sent by Dr. J. C. Arthur, of Purdue University. It could be seen that the rust was unquestionably *P. graminis secalis*. The reason for the failure on the one rye leaf inoculated directly with æciospores was that this leaf died early, thus making the trial inconclusive. However, the subsequent infection on rye as a result of inoculations

from *B. vulgaris* was very severe, clearly establishing the identity of the rust.

DIAGRAM 12.—Results of inoculations with æciospores developed on *Berberis vulgaris* from inoculations with teliospores from *Sporobolus cryptandrus* (Torr.) Gray.



[a] Leaves died early; inconclusive.

TABLE XXVI.—*Results of inoculations with urediniospores from Triticum compactum Host*

No.	Place.	Date.	*Triticum vulgare.*	*Avena sativa.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron tenerum.*
1	Pullman, Wash.[a].....	1916. Oct. 21	[b] 5/31; 1	.....	[c] 7/25	0/25	[c] 7/48

[a] Old spore material; many spores probably not viable.
[b] Hypersensitive.
[c] Normal infection.

The low percentage of infection from *Triticum compactum* is probably due to the fact that inoculations were made about a month after the rust was collected, and many of the spores had very probably lost their viability (Table XXVI).

It is not known whether all of the rust on club wheat west of the Rocky Mountains is of this type, since it is also susceptible to ordinary *P. graminis tritici;* but, on account of the absence of ordinary *P. graminis tritici* from grasses on which it would be expected to occur and on account of the prevalence of the club-wheat form on those grasses, it is probable that by far the greatest amount of rust on club wheat west of the mountains is *P. graminis tritici compacti.*

Only a few inoculations were made directly from wheat. These represent only a very small proportion of the total number of inoculations made with *P. graminis tritici.* Further inoculations were made with the rust, developed as a result of the inoculations reported in Table XXVII, but the results were of no particular interest, since they did not differ from any of those previously obtained.

It is quite apparent that in the upper Mississippi Valley and northern Great Plains area there are at least five biologic forms of *Puccinia graminis,* if *P. phleipratensis* be considered a biologic form, which seems quite justifiable—viz, *P. graminis tritici, P. graminis secalis, P. graminis avenae, P. graminis agrostis,* and *P. graminis phleipratensis.* In addition to these may be mentioned the strain *P. graminis secalis* found on *Hystrix patula.* There is probably not sufficient reason for calling this

a distinct biologic form, although it is somewhat different from any other form studied.

TABLE XXVII.—*Results of inoculations with urediniospores from Triticum vulgare*

No.	Place.	Date.	*Triticum vulgare.*	*Hordeum vulgare.*	*Secale cereale.*	*Agropyron repens.*	*Elymus virginicus.*	*Elymus robustus.*
1	St. Paul, Minn.	1915. May 22	.....	33/35	2/34	.....	23/26	31/32
2	Manhattan, Kans.	1916. June 3	44/53	11/12	2/16	.....	.....	.....
3	Denver, Colo.	Aug. 5	9/16	.....	0/19	0/9	.....	.....
4	Leederville, West Australia [a]	1917. Feb. 7	[b] 6/11	13/14	0/6; 1	.....	.....	.....

[a] One generation on club wheat in greenhouse before inoculations were made.
[b] Normal infection.

In the Palouse country of Washington and Idaho there is a common form resembling *P. graminis tritici* in many respects, but still very distinct from it. There seems sufficient reason for considering this a distinct biologic form for which the name "*Puccinia graminis tritici compacti*" is suggested.

Except for the variations mentioned, all of the rusts collected could be referred to one of the ordinary biologic forms, although there were sometimes slight differences in virulence. In general, however, the results of inoculations with different strains of a biologic form were monotonously uniform.

The results show very clearly, however, that the forms of stemrust which attack cereals commonly occur on many wild grasses over a large area.

After the identity of the different strains of biologic forms isolated from grasses or cereals from the field had been established inoculations were made on cereals and grasses, in order to determine whether the behavior was always constant.

KEY TO TABLES XXVIII–XXXIII

In Table XXVIII, and those following, "Original host" refers to the host on which the rust was collected in the field; "Immediate host" refers to the host from which spores were taken for inoculation; "Trials" refers to the number of different sets of inoculations made, plus (+) indicating the number of trials in which some plants became infected and minus (−) the number of entirely unsuccessful trials. The results are given in the form of a fraction, the denominator denoting the total number of leaves inoculated in all trials and the numerator the number which became infected.

TABLE XXVIII.—*Results of inoculations with urediniospores of Puccinia graminis tritici*

Original host.	Immediate host.	Plant inoculated.	Trials.		Result.	Degree of infection.
			+	−		
Triticum vulgare	*Triticum vulgare*	*Agropyron caninum*	2	0	3/75	Moderate.
Hordeum jubatum	*Hordeum vulgare*	do	0	2	0/70	
Do	*Triticum vulgare*	do	0	1	0/12	
Agropyron tenerum	*Hordeum vulgare*	*Agropyron cristatum*	0	1	0/6	
Hordeum jubatum	do	do	2	1	9/53	Do.
Do	do	*Agropyron desertorum*	0	2	0/33	
Do	do	*Agropyron elongatum*	1	0	15/18	Do.
Agropyron tenerum	do	*Agropyron imbricatum*	0	1	0/24	
Hordeum jubatum	*Agropyron tenerum*	do	0	1	0/3	
Do	*Hordeum vulgare*	do	0	1	0/31	
Do	do	*Agropyron intermedium*	1	1	2/26	Weak to moderate.
Agropyron smithii	do	do	1	0	1/27	Weak.
Hordeum jubatum	do	*Agropyron repens*	14	3	81/465	Do.
Do	*Triticum vulgare*	do	1	1	9/47	Do.
Agropyron smithii	*Hordeum vulgare*	do	3	2	14/141	Do.
Agropyron tenerum	do	do	2	1	6/84	Do.
Do	*Elymus virginicus*	do	1	0	1/31	Do.
Agropyron smithii	*Hordeum jubatum*	do	0	1	0/22	
Agropyron cristatum	*Hordeum vulgare*	do	2	0	14/107	Do.
Hordeum jubatum	*Agropyron smithii*	do	2	0	4/48	Do.
Agropyron cristatum	*Agropyron tenerum*	do	1	0	2/14	Do.
Do	*Hordeum vulgare*	do	1	0	1/14	Do.
Hordeum jubatum	*Agropyron repens*	do	2	0	8/38	Do.
Agropyron tenerum	*Agropyron smithii*	do	1	0	1/30	Do.
Hordeum jubatum	do	*Agropyron sibericum*	0	1	0/14	
Do	*Hordeum vulgare*	do	0	1	0/20	
Do	*Agropyron tenerum*	do	0	1	0/3	
Do	*Hordeum vulgare*	*Agropyron smithii*	6	0	47/140	Moderate to heavy.

TABLE XXVIII.—*Results of inoculations with urediniospores of Puccinia graminis tritici*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Agropyron smithii	*Hordeum vulgare*	*Agropyron smithii*	2	0	10/13	Heavy.
Agropyron cristatum	do	do	1	0	3/5	Do.
Hordeum jubatum	do	*Agropyron tenerum*	4	2	113/221	Moderate to heavy.
Do	*Triticum vulgare*	do	3	1	170/185	Heavy.
Agropyron tenerum	*Hordeum vulgare*	do	2	0	44/44	Do.
Do	*Elymus virginicus*	do	1	0	16/16	Do.
Agropyron smithii	*Hordeum vulgare*	do	2	0	67/67	Do.
Agropyron cristatum	do	do	2	0	49/49	Do.
Hordeum jubatum	do	*Agrostis alba*	0	1	0/150	
Agropyron smithii	*Hordeum jubatum*	do	0	1	0/70	
Triticum vulgare	*Triticum vulgare*	do	0	1	0/40	
Hordeum jubatum	*Hordeum vulgare*	*Agrostis stolonifera*	0	1	0/16	
Triticum vulgare	*Triticum vulgare*	do	0	1	0/68	
Hordeum jubatum	*Hordeum vulgare*	*Alopecurus geniculatus*	0	1	0/24	
Do	do	*Alopecurus pratensis*	1	1	3/130	Weak.
Agropyron tenerum	do	do	1	0	3/38	Do.
Triticum vulgare	*Triticum vulgare*	do	0	1	0/40	
Do	do	*Anthoxanthum odoratum*	0	1	0/60	
Hordeum jubatum	*Hordeum vulgare*	*Avena sativa*	5	6	8/372	Do.
Do	*Triticum vulgare*	do	1	2	2/111	Do.
Do	*Bromus tectorum*	do	0	3	0/54	
Agropyron smithii	*Hordeum vulgare*	do	0	2	0/26	
Agropyron tenerum	do	do	0	2	0/64	Do.
Triticum vulgare	*Triticum vulgare*	do	1	2	1/113	
Hordeum jubatum	*Hordeum vulgare*	*Beckmannia erucaeformis*	0	1	0/10	
Do	do	*Bouteloua curtipendula*	0	1	0/14	
Do	*Triticum vulgare*	*Bromus erectus*	0	1	0/9	
Do	*Hordeum vulgare*	do	0	1	0/17	

TABLE XXVIII.—*Results of inoculations with urediniospores of Puccinia graminis tritici*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Hordeum jubatum	*Triticum vulgare*	*Bromus hordeaceus*	1	0	2/17	Weak.
Agropyron tenerum	*Bromus tectorum*	do	0	1	0/8	
Hordeum jubatum	*Agropyron tenerum*	do	1	0	6/18	Moderate.
Do	*Triticum vulgare*	*Bromus inermis*	0	2	0/48	
Agropyron tenerum	*Hordeum vulgare*	*Bromus pumila*	1	0	14/16	Weak.
Hordeum jubatum	do	do	1	0	8/20	Do.
Do	do	*Bromus tectorum*	3	0	123/168	Light.
Do	*Triticum vulgare*	do	1	0	70/70	Do.
Agropyron tenerum	*Hordeum vulgare*	do	1	0	39/39	Do.
Hordeum jubatum	*Bromus tectorum*	do	1	0	18/25	Do.
Agropyron tenerum	do	do	2	0	25/36	Do.
Agropyron smithii	*Hordeum vulgare*	do	2	0	17/25	Weak.
Do	*Bromus tectorum*	do	0	1	0/5	
Hordeum jubatum	*Hordeum vulgare*	*Calamagrostis canadensis*	0	1	0/12	
Triticum vulgare	*Triticum vulgare*	*Cynodon dactylon*	0	1	0/4	
Hordeum jubatum	*Hordeum vulgare*	*Cynosurus cristatus*	0	1	0/22	
Do	do	*Dactylis glomerata*	1	1	1/60	Do.
Do	*Bromus tectorum*	do	1	0	1/15	Do.
Do	*Triticum vulgare*	*Elymus canadensis*	1	0	28/28	Heavy.
Do	*Hordeum vulgare*	do	2	0	38/48	Do.
Do	*Elymus canadensis*	do	2	0	98/98	Do.
Elymus canadensis	*Triticum vulgare*	do	1	0	25/25	Do.
Agropyron smithii	do	do	1	0	44/44	Do.
Triticum vulgare	do	*Elymus robustus*	1	0	31/32	Do.
Do	*Elymus robustus*	do	2	0	57/62	Do.
Hordeum jubatum	*Hordeum vulgare*	do	4	0	84/100	Do.
Do	*Triticum vulgare*	*Elymus virginicus*	1	0	30/34	Do.
Do	*Hordeum vulgare*	do	3	0	29/60	Moderate to heavy.

TABLE XXVIII.—*Results of inoculations with urediniospores of Puccinia graminis tritici*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Agropyron tenerum	*Hordeum vulgare*	*Elymus virginicus*	1	0	35/35	Heavy.
Agropyron smithii	do	do	1	0	32/32	Do.
Hordeum jubatum	do	*Festuca ovina*	0	1	0/20	
Do	do	*Festuca rubra*	0	1	0/31	
Triticum vulgare	*Triticum vulgare*	*Holcus lanatus*	0	1	0/44	
Hordeum jubatum	*Hordeum vulgare*	*Hordeum jubatum*	2	0	14/20	Do.
Do	*Elymus canadensis*	do	1	0	10/11	Do.
Do	*Triticum vulgare*	do	1	0	6/20	Do.
Agropyron tenerum	*Hordeum vulgare*	do	1	0	33/33	Do
Agropyron smithii	do	do	2	0	76/76	Do.
Hordeum jubatum	do	*Hordeum pusillum*	2	0	80/80	Do.
Agropyron tenerum	do	do	1	0	14/14	Do.
Hordeum jubatum	do	*Hordeum spontaneum*	1	0	8/10	Moderate.
Various	Various	*Hordeum vulgare*	X	0	4296/4503	Heavy.
Hordeum jubatum	*Hordeum vulgare*	*Hordeum vulgare* (Abyssinian).	3	0	60/75	Moderate.
Do	do	*Hordeum vulgare pallidum.*	1	0	25/27	Do.
Do	do	*Hordeum vulgare pallidum* subvar. *pyramidatum.*	1	0	11/32	Do.
Do	do	*Hystrix patula*	1	0	8/37	Do.
Agropyron tenerum	do	do	1	0	9/18	Do.
Hordeum jubatum	*Triticum vulgare*	*Koeleria cristata*	0	1	0/45	
Do	do	*Lolium italicum*	0	1	0/24	
Do	do	*Lolium perenne*	0	1	0/24	
Do	do	*Lolium temulentum*	0	1	0/23	
Do	*Hordeum vulgare*	*Poa nemoralis*	0	1	0/45	
Do	do	Secale cereale [a]	12	10	62/795	Weak.
Do	*Triticum vulgare*	do	2	0	9/120	Do.
Do	*Secale cereale*	do	5	6	12/91	Do.
Do	*Hordeum vulgare*	*Triticum compactum*	1	0	14/14	Heavy.

[a] The results recorded for *Secale cereale* represent only a small percentage of the total number of inoculations. These results will be given in another paper.

TABLE XXVIII.—*Results of inoculations with urediniospores of Puccinia graminis tritici*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Triticum vulgare	*Triticum vulgare*	*Triticum compactum*	2	0	34/40	Heavy.
Do	do	*Triticum dicoccum*	2	0	10/30	Weak.
Hordeum jubatum	*Hordeum vulgare*	do	1	0	3/4	Do.
Do	do	*Triticum durum*	4	0	14/14	Varies with variety.
Triticum vulgare	*Triticum vulgare*	do	3	0	27/44	Do.
Do	do	*Triticum monococcum*	0	1	0/5	
Hordeum jubatum	*Hordeum vulgare*	do	1	0	2/6	Weak.
Do	do	*Triticum polonicum*	1	0	3/3	Heavy.
Do	do	*Triticum speltum*	1	0	9/16	Weak.
Do	do	*Triticum turgidum*	1	0	6/7	Moderate.
Do	do	*Triticum vulgare* [a]	X	0	100 per cent.	Heavy.

[a] A very large number of inoculations were made with many wheat rust strains. Nearly always 100 per cent of the leaves became heavily infected.

The following summary can be made from the results obtained. The results of inoculations with rust from the various species of Triticum listed below are not given in the tables, since the results were so obviously what would be expected, and in one or two cases the inoculations were not actually made.

Hosts found infected in nature: *Agropyron caninum* (L.) Beauv., *A. cristatum* J. Gaert., *A. smithii* Rydb., *A. spicatum* (Pursh,) Rydb., *A. tenerum* Vasey, *Elymus brachystachys* Scribn. and Ball, *E. canadensis* L., *E. macounii* Vasey, *E. robustus* Scribn. and J. G. Sm., *E. virginicus* L., *Hordeum caespitosum* Scribn., *H. jubatum* L., *H. pusillum* Nutt., *H. vulgare* L., *Hystrix patula* Moench., *Secale cereale* L., *Triticum compactum* Host., *T. dicoccum* Schr., *T. durum* Desf., *T. monococcum* L., *T. polonicum* L., *T. spelta* L., *T. turgidum* L., *T. vulgare* Vill.

Hosts easily infected artificially: *Agropyron elongatum* Host., *Bromus hordeaceus* L., *B. pumila*, *B. tectorum* L., *Hordeum spontaneum* K. Koch., *H. vulgare* (Abyssinian), *H. vulgare pallidum* Ser., *H. vulgare pallidum* subvar. *pyramidatum*.

Weakly infected as a result of artificial inoculation: *Agropyron intermedium* Beauv., *A. repens* (L.) Beauv., *Alopecurus pratensis* L., *Avena sativa* L., *Secale cereale* L.

Inoculated but not infected: *Agropyron desertorum* Schult., *A. imbricatum* Roem. and Schult., *A. sibericum* Beauv., *Agrostis alba* L., *A. sto-*

lonifera Vasey, *Alopecurus geniculatus* L., *Anthoxanthum odoratum* L., *Beckmannia erucaeformis* (L.) Host., *Bromus erectus* Huds., *B. inermis* Leyss., *Calamagrostis canadensis* (Michx.) Beauv., *Cynodon dactylon* (L.) Pers., *Cynosurus cristatus* L., *Festuca ovina* L., *F. rubra* L., *Holcus lanatus* L., *Koeleria cristata* (L.) Pers., *Lolium italicum* R. Br., *L. perenne* L., *L. temulentum* L., *Poa nemoralis* L.

The results obtained by the writers in the main substantiate and extend those previously obtained by Carleton (6, 7) in this country, who says (7, p. 16)—

(1) that the forms of black stem rust on wheat, barley, *Hordeum jubatum*, *Agropyron tenerum*, *A. richardsoni*, *Elymus canadensis*, and *E. canadensis glaucifolius* are identical, with the probability that those on *Elymus virginicus*, *E. virginicus muticus*, and *Holcus lanatus* should be included; (2) that the black stem rust of *Agropyron occidentale* is physiologically distinct from any other.

The writers were unable to infect *Holcus lanatus*, although only a limited number of trials were made. *Agropyron smithii* (*A. occidentale*) is a very common host for both *P. graminis tritici* and *P. graminis secalis* in the upper Mississippi Valley. All the stemrust which the writers found was one of these two forms.

Eriksson (11, p. 601) gives *Triticum vulgare* as a host for wheat stemrust in Sweden, and states that barley, rye, and oats are sometimes weakly infected. The writers' results agree in general, except that barley is a very congenial host for the rust in this country, a fact previously noted by Carleton. Rye is weakly infected in a very characteristic manner. The production of uredinia in dead leaf areas (see pl. 53) is quite characteristic, although small uredinia may be produced without the killing of large areas. Rye is usually hypersensitive to the rust. Oats are infected rarely and with great difficulty.

Jaczewski (18, p. 353) gives *Triticum vulgare* as a host and says that *Hordeum vulgare*, *Triticum repens*, *T. caninum*, *Lolium perenne*, and *Festuca gigantea* can be infected, while *Secale cereale*, *Avena sativa*, *Dactylis glomerata*, *Bromus inermis*, and *B. secalinus* are immune. However, the writers have been able to infect both *Secale cereale* and *Avena sativa*.

In the spring-wheat-growing States some of the commonest grasses are very susceptible to wheat stemrust. The common species of Agropyron, except *A. repens*, are very congenial hosts. All of the species of Elymus and the closely related Hystrix which were tried are very susceptible, as well as the species of Hordeum. Of the cereals rye may rarely be affected with the rust in the field, and natural infection rarely, if ever, occurs on oats. Barley is very commonly affected, more often, probably, than with rye stemrust, to which it is also susceptible. *Bromus tectorum* is moderately susceptible, the uredinia usually remaining small and often round.

Only a few grasses besides the common hosts have been infected in the greenhouse. Oats and two of the grasses which are common hosts

for oat stemrust can be very rarely and weakly infected. On these hosts the uredinia were always very minute and often surrounded by an extremely small dead area.

There seem to be no marked differences in the rust on different hosts or in different parts of the upper Mississippi Valley and the northern Great Plains area. There appeared sometimes to be differences in virulence, but these were neither very constant nor very distinct. Rust on wheat kindly sent by Dr. F. Stoward from Leederville, West Australia, also behaved exactly like common *P. graminis tritici*. West of the Rocky Mountains, on the other hand, the rust on club wheat and grasses susceptible to *P. graminis tritici* is quite different, as previously noted.

TABLE XXIX.—*Results of inoculations with urediniospores of P. graminis tritici compacti*

Original host.	Immediate host.	Plant inoculated.	Trials.		Result.	Degree of infection.
			+	−		
Triticum compactum	*Triticum compactum*	*Agropyron cristatum*	1	0	14/24	Moderate.
Do	do	*Agropyron desertorum*	1	0	2/20	Weak.
Do	do	*Agropyron elongatum*	1	0	10/22	
Do	do	*Agropyron imbricatum*	0	1	0/30	Do.
Do	do	*Agropyron intermedium*	1	0	3/12	Do.
Do	*Hordeum vulgare*	*Agropyron repens*	1	0	2/22	Do.
Do	do	*Agropyron tenerum*	1	0	7/9	Moderate.
Do	*Triticum compactum*	do	1	0	10/20	Do.
Elymus glaucus	*Hordeum vulgare*	*Agrostis alba*	0	1	0/70	
Do	do	*Agropyron stolonifera*	0	1	0/35	
Triticum compactum	*Triticum compactum*	do	0	1	0/60	
Do	do	*Alopecurus geniculatus*	0	1	0/50	
Elymus glaucus	*Hordeum vulgare*	*Alopecurus pratensis*	0	1	0/38	
Triticum compactum	*Triticum compactum*	do	0	1	0/60	
Do	do	*Anthoxanthum odoratum*	0	1	0/70	
Elymus glaucus	*Hordeum vulgare*	do	0	1	0/75	
Do	do	*Avena sativa*	0	1	0/37	
Triticum compactum	*Triticum compactum*	do	0	2	0/75	
Elymus glaucus	*Hordeum vulgare*	do	0	2	0/38	
Triticum compactum	do	*Bromus tectorum*	1	0	40/40	Weak.

TABLE XXIX.—*Results of inoculations with urediniospores of P. graminis tritici compacti*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Triticum compactum	*Triticum compactum*	*Elymus canadensis*	1	0	20/20	Heavy.
Do	do	*Holcus lanatus*	0	1	0/50	
Do	do	*Hordeum jubatum*	1	0	30/30	Do.
Triticum compactum, *Elymus glaucus*	Various	*Hordeum vulgare*	12	0	305/336	Do.
Triticum compactum	*Triticum compactum*	*Koeleria cristata*	0	1	0/25	
Do	do	*Phleum pratense*	0	1	0/20	
Do	do	*Poa compressa*	0	1	0/15	
Elymus glaucus	*Secale cereale*	*Secale cereale*	0	1	0/14; 8	
Triticum compactum	*Triticum compactum*	do	2	0	3/29; 10	Weak.
Elymus glaucus	*Hordeum vulgare*	do	2	0	4/18; 3	Do.
Triticum compactum	*Triticum compactum*	*Triticum compactum*	7	0	238/242	Very heavy.
Do	*Hordeum vulgare*	do	1	0	34/34	Do.
Do	*Triticum vulgare*	do	1	0	10/12	Do.
Elymus glaucus	*Hordeum vulgare*	do	4	0	33/38	Do.
Elymus condensatus	*Triticum vulgare*	do	2	0	43/51	Do.
Do	*Triticum compactum*	do	2	0	106/109	Do.
Do	do	*Triticum dicoccum* [a]	2	0	38/43	Variable, mostly weak.
Elymus glaucus	*Hordeum vulgare*	do	3	0	24/36	Weak.
Triticum compactum	*Triticum compactum*	do	2	0	21/26	Do.
Elymus condensatus	do	*Triticum durum*	6	0	104/122	Weak to moderate.
Elymus glaucus	*Hordeum vulgare*	do	3	0	49/50	Moderate.
Do	do	*Triticum monococcum*	1	0	15/15	Heavy.
Elymus condensatus	*Triticum compactum*	do	2	0	24/39	Moderate to heavy.
Do	do	*Triticum vulgare*	6	0	128/136	Variable; mostly weak.
Triticum compactum	do	do	7	0	69/81	Do.
Do	*Hordeum vulgare*	do	2	0	14/69	Weak.
Do	*Triticum vulgare*	do	2	0	18/31	Do.
Elymus glaucus	*Hordeum vulgare*	do	11	0	161/177	Do.

[a] A number of different varieties of *Triticum dicoccum*, *T. durum*, *T. monococcum*, and *T. vulgare* were tried. There was sometimes a varietal difference in susceptibility.

The results of inoculations with *P. graminis tritici compacti* can be summarized as follows:

Hosts on which the rust has been found in nature: *Agropyron smithii* Rydb., *Elymus canadensis* L., *E. condensatus* Presl., *E. glaucus* Buckley, *E. macounii* Vasey, *Hordeum jubatum* L., *Triticum compactum* Host.

Hosts easily infected by artificial inoculation: *Agropyron cristatum* J. Gaert., *A. elongatum* Host., *A. tenerum* Vasey, *Bromus tectorum* L., *Hordeum vulgare* L., *Triticum durum* Desf. (some varieties), *Triticum monococcum* L., *T. vulgare* Vill. (a few varieties).

Weakly infected by artificial inoculation: *Agropyron desertorum* Schult., *A. intermedium* Beauv., *A. repens* (L.) Beauv., *Secale cereale* L., *Triticum dicoccum* Schr., *T. durum* Desf. (some varieties), *T. vulgare* Vill. (most varieties tried).

Artificially inoculated but not infected: *Agrostis alba* L., *A. stolonifera* Vasey, *Alopecurus geniculatus* L., *A. pratensis* L., *Anthoxanthum odoratum* L., *Avena sativa* L., *Holcus lanatus* L., *Koeleria cristata* (L.) Pers., *Phleum pratense* L., *Poa compressa* L.

It is quite evident that this rust is very similar in many respects to *P. graminis tritici*. However, its behavior on most varieties of *Triticum vulgare* so far inoculated is so very different from that of *P. graminis tritici* that it can scarcely be included in the latter form. All of the hard spring wheats, including Minnesota 169, Minnesota 163, Marquis, and Preston, are very resistant to *P. graminis tritici compacti*, showing a high degree of hypersensitiveness, while they are very susceptible to *P. graminis tritici*. (See Pl. 53–56.) The same is true of the hard winter wheats which have been inoculated. The soft wheats are, however, more susceptible. It is on account of its very distinctive action on the hard wheats of the *vulgare* group that it seems desirable to apply a distinct name in order to avoid confusion. The morphology of the urediniospores is also somewhat different from that of any of the other forms.

P. tritici compacti has been found only in the Palouse country, where it seems to be very common on wild grasses and on club wheats. Whether ordinary *P. graminis tritici* also occurs in that region, the writers have not yet been able to determine. All the rust collected on wild grasses and cereals was the *tritici compacti* form.

The degree of stability or fixity of the rust should be thoroughly investigated. It is possible that it is an easily changed variant strain of ordinary *P. graminis tritici*, although all attempts made by the writers to change its parasitic tendencies by confining it for a number of successive generations to an uncongenial host or by the use of possible bridging hosts have been unsuccessful.

TABLE XXX.—*Results of inoculations with urediniospores of Puccinia graminis secalis*

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Agropyron repens	*Hordeum vulgare*	*Agropyron caninum*	2	0	14/68	Moderate.
Hystrix patula	*Secale cereale*	do	1	0	1/3	Do.
Agropyron repens	*Hordeum vulgare*	*Agropyron cristatum*	1	0	26/28	Heavy.
Agropyron cristatum	do	do	1	0	3/15	Moderate.
Hordeum jubatum	do	do	2	0	29/42	Moderate to heavy.
Agropyron repens	do	*Agropyron desertorum*	0	2	0/22	
Secale cereale	*Secale cereale*	do	1	0	1/25	Weak.
Agropyron repens	*Hordeum vulgare*	*Agropyron imbricatum*	1	2	1/50	Do.
Secale cereale	*Secale cereale*	do	0	1	0/20	
Agropyron repens	*Hordeum vulgare*	*Agropyron intermedium*	0	1	0/6	
Secale cereale	*Secale cereale*	do	1	0	5/13	Do.
Agropyron smithii	do	*Agropyron repens*	1	0	34/34	Heavy.
Agropyron repens	do	do	1	0	13/32	Do.
Do	*Hordeum vulgare*	do	2	0	51/57	Do.
Do	*Agropyron repens*	do	1	0	10/12	Do.
Do	*Elymus canadensis*	do	1	0	23/23	Do.
Do	*Elymus robustus*	do	1	0	21/21	Do.
Secale cereale	*Secale cereale*	do	3	0	129/130	Do.
Hystrix patula	*Hordeum vulgare*	do	1	0	15/15	Do.
Agropyron repens	do	*Agropyron sibericum*	0	2	0/48	
Agropyron smithii	do	*Agropyron smithii*	2	0	10/12	Do.
Agropyron repens	do	do	2	0	17/61	Moderate.
Hordeum jubatum	do	do	1	0	6/6	Heavy.
Agropyron cristatum	*Secale cereale*	*Agropyron tenerum*	1	0	72/72	Do.
Do	*Hordeum vulgare*	do	1	0	16/16	Do.
Agropyron repens	do	do	2	0	12/63	Moderate.
Do	*Elymus virginicus*	do	1	0	62/78	Heavy.
Do	*Hordeum jubatum*	do	1	0	4/18	Light.

TABLE XXX.—*Results of inoculations with urediniospores of Puccinia graminis secalis*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials.		Result.	Degree of infection.
			+	−		
Agropyron repens	*Agropyron tenerum*	*Agropyron tenerum*	8	0	286/340	Moderate to heavy.
Hordeum jubatum	*Hordeum vulgare*	do	6	0	60/60	Heavy.
Hystrix patula	*Elymus virginicus*	do	1	0	52/60	Do.
Do	*Agropyron tenerum*	do	8	0	305/338	Moderate to heavy.
Agropyron repens	*Elymus virginicus*	*Agrostis alba*	0	1	0/50	
Secale cereale	*Secale cereale*	do	0	2	0/110	
Do	do	*Agrostis stolonifera*	0	1	0/65	
Hordeum jubatum	*Hordeum vulgare*	*Alopecurus geniculatus*	0	1	0/24	
Do	do	*Alopecurus pratensis*	0	1	0/70	
Secale cereale	*Secale cereale*	do	0	1	0/40	
Do	do	*Anthoxanthum odoratum*	0	1	0/45	
Agropyron repens	*Hordeum vulgare*	*Arrhenatherum elatius*	0	1	0/10	
Do	do	*Avena fatua*	0	1	0/10	
Do	do	*Avena sativa*	0	1	0/19	
Do	*Agropyron repens*	do	0	1	0/19	
Do	*Secale cereale*	do	0	1	0/14	
Secale cereale	*Hordeum vulgare*	do	1	2	3/101	
Do	*Secale cereale*	do	3	1	8/167	Weak.
Agropyron repens	*Elymus virginicus*	*Bromus purgans*	1	0	2/16	Do.
Do	*Hordeum vulgare*	*Bromus tectorum*	2	0	53/70	Light.
Secale cereale	*Secale cereale*	*Dactylis glomerata*	0	1	0/24	
Agropyron repens	*Hordeum jubatum*	do	0	1	0/12	
Do	*Secale cereale*	*Elymus canadensis*	1	0	26/27	Heavy.
Do	*Agropyron repens*	do	1	0	11/11	Do.
Do	*Hordeum vulgare*	do	1	0	17/17	Do.
Do	*Elymus canadensis*	do	11	0	328/371	
Do	*Hordeum vulgare*	do	1	0	7/12	Do.
Do	*Elymus robustus*	do	1	0	23/23	Do.

TABLE XXX.—*Results of inoculations with urediniospores of Puccinia graminis secalis*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Elymus canadensis	*Secale cereale*	*Elymus canadensis*	1	0	12/12	Heavy.
Agropyron repens	do	*Elymus robustus*	1	0	28/30	Do.
Do	*Hordeum vulgare*	do	2	0	35/35	Do.
Do	*Elymus robustus*	do	12	0	233/264	Do.
Do	*Secale cereale*	*Elymus virginicus*	1	0	23/29	Do.
Do	*Agropyron repens*	do	1	0	6/7	Do.
Do	*Elymus virginicus*	do	11	0	414/436	Moderate to heavy.
Do	*Hordeum vulgare*	do	2	0	30/35	Heavy.
Do	*Elymus canadensis*	do	1	0	7/7	Do.
Do	*Hordeum jubatum*	do	1	0	7/15	Moderate.
Do	*Hordeum vulgare*	do	2	0	56/60	Heavy.
Hystrix patula	do	do	1	0	26/26	Do.
Do	*Elymus virginicus*	do	2	0	52/54	Do.
Secale cereale	*Secale cereale*	*Holcus lanatus*	0	1	0/26	
Agropyron repens	*Agropyron repens*	*Hordeum jubatum*	1	0	14/28	Do.
Do	*Elymus robustus*	do	2	0	13/34	Moderate.
Do	*Hordeum jubatum*	do	6	0	228/263	Heavy.
Do	*Elymus virginicus*	do	2	0	23/47	Light.
Hystrix patula	*Agropyron tenerum*	do	1	0	33/40	Heavy.
Do	*Hordeum jubatum*	do	5	0	142/184	Moderate to heavy.
Agropyron repens	*Elymus virginicus*	*Hordeum pusillum*	1	0	70/70	Moderate.
Do	*Hordeum vulgare*	*Hordeum vulgare* (Abyssinian).	3	0	49/57	Do.
Do	do	*Hordeum vulgare pallidum*, subvar. *pyramidatum*.	1	0	6/12	Do.
Do	do	*Hordeum spontaneum*	1	0	7/7	Do.
Do	do	*Hordeum vulgare pallidum*.	1	0	28/28	Do.
Do	*Elymus virginicus*	*Hystrix patula*	1	0	18/18	Do.
Hystrix patula	do	do	1	1	22/40	Heavy.
Agropyron repens	*Hordeum vulgare*	*Koeleria cristata*	0	1	0/30	

TABLE XXX.—*Results of inoculations with urediniospores of Puccinia graminis secalis*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials.		Result.	Degree of infection.
			+	−		
Agropyron repens	*Agropyron repens*	*Lolium perenne*	0	1	0/17	
Do	*Elymus virginicus*	do	0	1	0/19	
Do	*Hordeum vulgare*	*Phalaris canariensis*	0	1	0/19	
Do	do	*Triticum compactum*	0	1	0/24	
Do	do	*Triticum vulgare* [a]	3	12	3/454	
Do	*Elymus robustus*	do	0	5	0/147	
Do	*Elymus canadensis*	do	1	10	1/394	

[a] Only a few of the results with wheat are recorded here; they will appear later.

The results of the survey work and of the inoculations with known strains of *P. graminis secalis* can be summarized as follows: *P. graminis secalis* has been found on the following hosts in the field: *Agropyron caninum* (L.) Beauv., *A. cristatum* J. Gaert., *A. smithii* Rydb., *A. repens* (L.) Beauv., *A. tenerum* Vasey, *Elymus canadensis* L., *E. robustus* Scribn. and J. G. Sm., *Hordeum jubatum* L., *H. pusillum* Nutt., *H. vulgare* L., *Hystrix patula* Moench., *Secale cereale* L., *Sporobolus cryptandrus* (Torr.) Gray.

In addition to the above, the following have been easily infected by artificial inoculation: *Agropyron elongatum* Host., *Bromus tectorum* L., *Elymus virginicus* L., *Hordeum spontaneum* K. Koch, *H. vulgare pallidum* Ser., *H. vulgare pallidum* subvar. *pyramidatum*.

The following have been weakly infected artificially: *Agropyron imbricatum* Roem., and Schult., *A. intermedium* Beauv., *A. sibericum* Beauv., *Avena sativa* L., *Bromus purgans* L., *Triticum vulgare* Vill.

Inoculated but not infected: *Agropyron desertorum* Schult., *Agrostis alba* L., *A. stolonifera* Vasey, *Alopecurus geniculatus* L., *A. pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) Beauv., *Avena fatua* L., *Dactylis glomerata* L., *Holcus lanatus* L., *Koeleria cristata* (L.) Pers., *Lolium perenne* L., *Phalaris canariensis* L., *Triticum compactum* Host.

Little work has been done on the wild hosts for *P. graminis secalis* in this country. Carleton (6. p. 60) reports successful infection of rye and barley, but not of wheat, with—

> what seemed to be uredospores of *P. graminis* from *Hordeum jubatum*

and concludes in a preliminary way that *Hordeum jubatum* supports two distinct forms of *P. graminis*. These two forms, in the light of the writers'

experiments, are *P. graminis tritici* and *P. graminis secalis*, both of which infect *H. jubatum* easily and both of which are commonly found on the grass in the field. Freeman and Johnson (14, p. 21, 28) showed that stemrust of rye infects both rye and barley, but did not work with the grass hosts. Pritchard (22, p. 181), as a result of work done in North Dakota, concludes—

> that one form of *P. graminis* is common to *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, *Avena fatua*, oats, and rye, but is incapable of infecting either barley or wheat.

Pritchard very probably worked with two forms—viz, (1) *P. graminis secalis*, which probably caused the infection of *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, and rye; and (2) *P. graminis avenae*, which infected the oats, and *A. fatua*.

In Sweden Eriksson (11, p. 601) did considerable work on the grass hosts of rye stemrust, and gives the following as hosts:

> *Secale cereale*, *Hordeum vulgare*, *H. jubatum*, *H. murinum*, *H. comosum*, *Triticum repens*, *T. caninum*, *T. desertorum*, *Elymus arenarius*, *E. sibericus*, and *Bromus secalinus*.

It is quite apparent that this rust in Sweden is very similar, if not identical, with that in this country. Eriksson mentions *Triticum* (*Agropyron*) *desertorum* as a host; the writers were not able to infect this host in the greenhouse, but the number of trials was too small to justify definite conclusions. While the species of grasses with which Eriksson and the writers worked are not all the same, the same genera were investigated, and some species of these genera were found as hosts for the rusts in both countries. It is very probable, although by no means certain, that most of the species of Agropyron, Hordeum, Elymus, and Hystrix are susceptible to rye stemrust.

Jaczewski's results in Russia do not agree closely with those of Eriksson nor those recorded in this paper. He mentions *Secale cereale* (18, p. 353) as the host, and states that the rust is capable of infecting *Triticum repens*, *T. caninum*, and *Dactylis glomerata*. The writers were unable to infect *D. glomerata* with stemrust of rye, although only 46 leaves were inoculated. It is entirely possible that the rust can infect *D. glomerata* weakly, but it is improbable that it does so commonly enough to be of practical significance. Jaczewski states that *Hordeum vulgare* is immune to the rust. In this country it is very susceptible.

The stemrust of rye in this country easily infects rye and barley, but very rarely, or scarcely at all, wheat and oats. Of the wild grass hosts *Agropyron repens* is by far the most common. It is nearly always severely affected. Although *A. repens* can be infected weakly by *P. graminis tritici* also, it is doubtful if the wheat stemrust occurs on it, unless quite exceptionally, in the field. In general the various species of Agropyron, Elymus, Hordeum, and Hystrix are hosts for the rust. It is found commonly on at least some species of all these genera in the field.

It is noteworthy that the stemrust of rye and the stemrust of wheat have so many hosts in common, especially since wheat is practically immune to *P. graminis secalis* and rye is very highly resistant to *P. graminis tritici*.

TABLE XXXI.—*Results of inoculations with urediniospores of P. graminis avenae*

Original host.	Immediate host.	Plant inoculated.	Trials.		Result.	Degree of infection.
			+	−		
Dactylis glomerata	*Avena sativa*	*Agropyron caninum*	0	3	0/61	
Do	do	*Agropyron cristatum*	1	0	3/25	
Do	do	*Agropyron desertorum*	0	1	0/30	
Bo	do	*Agropyron elongatum*	0	1	0/25	
Do	do	*Agropyron imbricatum*	0	1	0/20	
Do	do	*Agropyron intermedium*	0	1	0/25	
Do	do	*Agropyron repens*	0	3	0/93	
Do	do	*Agropyron smithii*	0	4	0/54	
Do	do	*Agropyron tenerum*	0	2	0/35	
Do	do	*Agrostis alba*	1	1	30/480	Moderate.
Agrostis exarata	do	do	1	0	7/30	Light.
Dactylis glomerata	do	*Agrostis stolonifera*	0	3	0/123	Strong flecks
Avena sativa	do	do	0	1	0/40	
Agrostis exarata	do	do	3	0	21/100	Light to moderate.
Panicularia pauciflora	do	do	1	0	5/10	Moderate.
Dactylis glomerata	do	*Alopecurus geniculatus*	1	0	27/35	Do.
Agrostis exarata	do	do	1	0	30/42	Do.
Dactylis glomerata	do	*Alopecurus pratensis*	2	1	119/105	Heavy.
Agrostis exarata	do	do	1	0	35/35	Moderate.
Dactylis glomerata	do	*Anthoxanthum odoratum*	2	2	76/183	Do.
Do	do	*Arrhenatherum elatius*	4	2	17/200	Light to moderate.
Do	*Avena fatua*	do	1	0	2/11	Light.
Do	*Avena sativa*	*Avena fatua*	1	0	43/44	Heavy.
Do	*Avena fatua*	do	1	0	40/40	Do.
Do	*Avena sativa*	*Beckmannia erucaeformis.*	1	0	1/17	Small uredinium.
Avena sativa	do	do	0	1	0/9	

TABLE XXXI.—*Results of inoculations with urediniospores of P. graminis avenae*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Dactylis glomerata	*Avena sativa*	*Bromus erectus*	1	1	1/17	Light.
Do	*Bromus tectorum*	do	1	0	2/18	Do.
Do	*Avena sativa*	*Bromus hordeaceus*	0	1	0/8	
Do	*Bromus tectorum*	do	0	1	0/34	
Do	*Avena sativa*	*Bromus inermis*	0	1	0/40	
Avena sativa	do	*Bromus pumila*	0	1	0/10	
Dactylis glomerata	do	*Bromus purgans*	1	0	1/23	Do.
Do	do	*Bromus tectorum*	5	0	194/194	Light to moderate.
Do	do	*Calamagrostis canadensis.*	1	0	2/13	Moderate.
Avena sativa	do	do	0	1	0/12	
Panicularia pauciflora	do	do	1	0	12/15	Do.
Agrostis exarata	do	do	1	0	20/25	
Dactylis glomerata	do	*Cynodon dactylon*	0	1	0/14	
Do	do	*Cynosurus cristatus*	0	2	0/60	
Avena sativa	do	do	0	1	0/30	
Dactylis glomerata	do	*Dactylis glomerata*	3	0	51/79	Heavy.
Panicularia pauciflora	do	do	1	0	7/7	Do.
Agrostis exarata	do	do	1	0	12/12	Do.
Avena sativa	do	*Danthonia spicata*	0	1	0/36	
Do	do	*Deschampsia flexuosa*	0	1	0/3	
Dactylis glomerata	*Avena fatua*	*Elymus canadensis*	1	0	2/20	Small uredinia.
Do	*Avena sativa*	do	3	3	14/265	Weak.
Do	*Avena fatua*	*Elymus robustus*	1	0	1/20	Small uredinium.
Do	*Avena sativa*	do	3	2	3/138	Do.
Do	*Avena fatua*	*Elymus virginicus*	0	1	0/20	
Do	*Avena sativa*	do	0	4	0/140	
Do	do	*Festuca elatior*	3	0	11/163	Weak.
Avena sativa	do	do	1	0	1/21	Do.
Dactylis glomerata	do	*Festuca ovina*	1	1	4/37	Moderate.

TABLE XXXI.—*Results of inoculations with urediniospores of P. graminis avenae*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials.		Result.	Degree of infection.
			+	−		
Avena sativa	*Avena sativa*	*Festuca ovina*	0	1	0/17	
Dactylis glomerata	do	*Festuca rubra*	0	1	0/17	
Avena sativa	do	do	0	1	0/28	
Dactylis glomerata	do	do	0	2	0/30	
Do	do	*Holcus lanatus*	2	1	55/190	Moderate.
Avena sativa	do	do	1	0	1/13	Small uredinium.
Agrostis exarata	do	do	1	0	25/30	Moderate.
Dactylis glomerata	do	*Hordeum jubatum*	0	2	0/55	
Do	do	*Hordeum pusillum*	1	0	4/28	Small uredinia.
Do	do	*Hordeum spontaneum*	1	0	3/6	Minute uredinia.
Do	do	*Hordeum vulgare*	14	2	27/471	Do.
Do	*Avena fatua*	do	1	0	1/36	Do.
Do	*Koeleria cristata*	do	0	1	0/13	
Do	*Bromus tectorum*	do	1	0	3/36	Do.
Avena sativa	do	do	1	0	3/26	Small uredinia.
Panicularia pauciflora	*Avena sativa*	do	1	0	12/14	Heavy.
Agrostis exarata	do	do	1	0	11/16	Moderate.
Anthoxanthum puelii	do	do	1	0	9/13	Minute uredinia.
Panicularia pauciflora	*Hordeum vulgare*	do	1	1	3/53	
Dactylis glomerata	*Avena sativa*	*Hordeum vulgare* (Abyssinian).	1	2	1/42	Do.
Do	do	*Hordeum vulgare pallidum.*	0	1	0/11	
Do	do	*Hordeum vulgare Pallidum* subvar. *pyramidatum.*	0	1	0/19	
Do	do	*Hystrix patula*	1	0	1/19	Small uredinia.
Do	do	*Koeleria cristata*	1	0	15/20	Heavy.
Do	*Avena fatua*	*Lolium italicum*	0	1	0/22	
Do	*Avena sativa*	do	1	2	2/151	Weak.
Do	do	*Lolium perenne*	2	2	5/191	Do.
Do	do	*Lolium temulentum*	2	0	16/55	Moderate.

TABLE XXXI.—*Results of inoculations with urediniospores of P. graminis avenae*—Continued

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Dactylis glomerata	*Avena sativa*	*Phalaris canariensis*	1	0	17/19	Moderate.
Agrostis exarata	*Dactylis glomerata*	*Phleum pratense*	1	0	1/15	Weak.
Anthoxanthum puelii	*Avena sativa*	do	1	0	3/79	Do.
Dactylis glomerata	do	do	1	0	5/50	Do.
Panicularia pauciflora	*Dactylis glomerata*	do	1	0	7/35	Do.
Do	*Phleum pratense*	do	0	1	0/7	
Dactylis glomerata	*Avena sativa*	*Poa nemoralis*	0	1	0/10	
Do	do	*Poa compressa*	0	2	0/44	
Do	do	*Savastana odorata*	0	1	0/6	
Avena sativa	do	do	0	1	0/15	
Dactylis glomerata	do	*Secale cereale*	3	4	9/301	Minute uredinia.
Do	*Avena fatua*	do	1	0	4/34	Do.
Do	*Bromus tectorum*	do	0	1	0/17	
Agrostis exarata	*Avena sativa*	do	0	1	0/11; 3	
Panicularia pauciflora	do	do	3	0	8/50	Do.
Dactylis glomerata	do	*Triticum vulgare*	0	9	0/431	
Panicularia pauciflora	do	do	0	2	0/26	

The results of the field-survey work and inoculations in the greenhouse with *P. graminis avenae* are given in the following summary:

Hosts found naturally infected: *Avena sativa* L., *A. fatua* L., *Agrostis exarata* Trin., *Anthoxanthum puelli* Lecoq. and Lamotte, *Dactylis glomerata* L., *Koeleria cristata* (L.) Pers., *Panicularia pauciflora* (Presl.) Kuntze.

Easily infected by artificial inoculation: *Arrhenatherum elatius* (L.) Beauv., *Alopecurus geniculatus* L., *A. pratensis* L., *Bromus tectorum* L., *Calamagrostis canadensis* (Michx.) Beauv., *Holcus lanatus* L., *Phalaris canariensis* L.

Weakly infected by artificial inoculation: *Agropyron cristatum* J. Gaert., *Agrostis alba* L., *A. stolonifera* Vasey, *Beckmannia erucaeformis* (L.) Host., *Bromus erectus* Huds., *B. purgans* L., *Elymus canadensis* L., *E. robustus* Scribn. and J. G. Sm., *Festuca elatior* L., *F. ovina* L., *Hordeum pusillum* Nutt., *H. vulgare* L., *H. vulgare pallidum* Ser., *H. vulgare*

pallidum subvar. *pyramidatum*, *H. spontaneum* K. Koch, *Hystrix patula* Moench., *Lolium italicum* R. Br., *L. perenne* L., *L. temulentum* L., *Phleum pratense* L., *Secale cereale* L.

Inoculated but not infected: *Agropyron caninum* (L.) Beauv., *A. desertorum* Schult., *A. elongatum* Host., *A. imbricatum* Roem. and Schult., *A. intermedium* Beauv., *A. repens* (L.) Beauv., *A. smithii* Rydb., *A. tenerum* Vasey, *Bromus inermis* Leyss., *B. pumila*, *Cynodon dactylon* (L.) Pers., *Cynosurus cristatus* L., *Danthonia spicata* (L.) Beauv., *Deschampsia flexuosa* (L.) Trin., *Elymus virginicus* L., *Festuca rubra* L., *Hordeum jubatum* L., *H. spontaneum* K. Koch, *H. vulgare pallidum* Ser. *H. vulgare pallidum* subvar. *pyramidatum*, *Poa compressa* L., *Savastana odorata* (L.) Scribn., *Triticum vulgare* Vill.

Carleton (6, p. 63–64) gives the following as hosts for stemrust of oats: *Avena sativa patula*, *A. sativa orientalis*, and *A. sativa nuda* (cultivated varieties and *Dactylis glomerata* and *Arrhenatherum elatius*. The following he considers as probable hosts: *Avena fatua*, *A. hookeri*, *A. pratensis*, *A. sterilis*, *Koeleria cristata* and *Lolium perenne*. The writers have shown that *A. fatua*, and *Koeleria cristata* are undoubtedly hosts and that *Lolium perenne* can be infected, although whether or not it is commonly a host has not been determined. Carleton's results and those of the writers are in general agreement with those of Eriksson (11, p. 601) in Sweden, although the same species were not used in inoculation experiments in all cases. Jaczewski (18, p. 353), on the other hand, arrived at different conclusions as a result of his work in Russia. The most striking difference is that he gives *Dactylis glomerata* as immune, whereas in this country it is one of the very common hosts. Eriksson and Henning also give it as one of the hosts in Sweden. It would be interesting to know whether the rust is really different in Russia or whether for some reason *D. glomerata* did not become infected in the limited number of trials which Jaczewski made.

A number of investigators have called attention to the versatility of the oat stemrust. There is no doubt that it can infect many different grasses.

It is interesting to notice the varying degrees of virulence of the rust on different hosts. It is extremely virulent on such hosts as *Avena sativa*, *A. fatua*, and *Dactylis glomerata*, while on *Alopecurus pratensis* it is moderately virulent, on *Holcus lanatus* a little less virulent, on *Agrostis alba* still less virulent, on *Hordeum vulgare* and *Secale cereale* it develops very imperfectly, and on *Triticum vulgare* it scarcely ever even produces flecks.

The stemrust of oats is similar to *P. phleipratensis* and *P. graminis agrostis* in its ability to infect plants in such varying degrees. (See Pl. 57–59.) The other biologic forms do not seem to behave in this way. The wheat stemrust and the rye stemrust sometimes infect plants weakly, but, as a rule, they either cause heavy infection or none at all.

The facts cited above raise an interesting question which the writers have not yet been able to answer—namely, Is *P. graminis avenae* a plastic form or is it a composite form from which the component forms can be isolated by culture on various hosts? Morphological studies of the stemrust of oats made by Mr. M. N. Levine, of this Station, not yet published, show that *P. graminis avenae* is very variable morphologically, more variable than any of the other biologic forms. Spores practically indistinguishable from those of *P. phleipratensis*, and others very similar to those of *P. graminis agrostis*, are commonly produced by *P. graminis avenae*. The infection capabilities of the three rusts are similar. These facts may be of some significance, but, at present, speculation only is possible.

Stemrust of oats was found very commonly in the region covered by the survey. It was very prevalent on grasses in the western mountain valleys, and, on account of the large number of possible hosts, it is quite probable that grasses are quite important in its spread and possibly as a means of its overwintering. Unfortunately no studies on this phase of the problem have yet been made. They are highly important and will be made as soon as possible.

TABLE XXXII.—*Results of inoculations with urediniospores of P. graminis phleipratensis*

Original host.	Immediate host.	Plant inoculated.	Trials.		Result.	Degree of infection.
			+	−		
Phleum pratense	*Phleum pratense*	*Agrostis alba*	0	2	0/165	
Festuca elatior	do	*Alopecurus geniculatus*	1	0	65/70	Moderate.
Do	do	*Alopecurus pratensis*	2	0	37/60	Moderate to heavy.
Do	do	*Avena sativa*	1	0	1/28	
Do	*Avena sativa*	do	5	2	22/96	Weak.
Phleum pratense	*Phleum pratense*	*Festuca elatior*	1	0	36/36	Heavy.
Do	do	*Festuca ovina*	0	1	0/17	
Do	do	*Festuca rubra*	0	1	0/11	
Festuca elatior	do	*Holcus lanatus*	1	0	25/30	Moderate.
Do	do	*Hordeum vulgare*	1	0	7/29	
Festuca pratensis	*Hordeum vulgare*	do	2	3	14/50	Weak.
Festuca elatior	*Phleum pratense*	*Koeleria cristata*	1	0	35/40	Heavy.
Do	do	*Poa compressa*	0	1	0/15	
Do	do	*Secale cereale*	1	0	1/30	
Do	do	*Triticum vulgare*	0	1	0/22	

Hosts on which *P. graminis phleipratensis* was found in nature: *Dactylis glomerata* L., *Festuca elatior* L., *F. pratensis* Huds., *Koeleria cristata* (L.) Pers., *Phleum pratense* L.

Hosts heavily infected by artificial inoculation: *Alopecurus geniculatus* L., *A. pratensis* L., *Holcus lanatus* L.

Weakly infected by artificial inoculation: *Avena sativa* L., *A. fatua* L., *Arrhenatherum elatius* (L.) Beauv., *Bromus tectorum* L., *Elymus virginicus* L., *Hordeum jubatum* L., *H. vulgare* L., *Lolium italicum* R. Br., *L. perenne* L., *Secale cereale* L.

Inoculated but not infected: *Agropyron repens* (L.) Beauv., *Agrostis alba* L., *Festuca ovina* L., F. *rubra* L., *Poa compressa* L., *Triticum vulgare* Vill.

It will be observed that the timothy rust occurs in the field on *Dactylis glomerata*, *Festuca elatior*, and *F. pratensis* and probably *Koeleria cristata*, in addition to *Phleum pratense*. Eriksson and Henning (13, p. 130) give only *Phleum pratense* as a host plant, as does Johnson (19), although he succeeded in infecting *D. glomerata* and *F. elatior* by means of artificial inoculations. How commonly this rust occurs on *D. glomerata* the writers do not know; however, it does occur commonly on both species of Festuca mentioned.

The character of infection on the plants mentioned as weakly infected in the greenhouse has been previously discussed (26) and need not be repeated here.

The relation of the rust to *P. graminis* is still probably debatable. The problem has been summarized by Stakman and Jensen (26, p. 211). So far as the writers have been able to determine, no one has yet been able to infect barberry consistently with the teliospores. The writers made numerous inoculations in the spring and early summer of 1916 at a time when teliospores of the common biologic forms readily infected barberries, but no æcia developed as a result of the inoculations made with timothy-rust teliospores. Flecks were commonly developed, and, although histological examination was not made, it is quite probable that infection occurred, but the rust was unable to develop æcia. On morphological grounds there seems to be no justification for regarding timothy rust as a distinct species; it does not differ more from ordinary biologic forms of *P. graminis* than does *P. graminis agrostis*. The same is true of its infection capabilities. The writers favor including it as a biologic form of *P. graminis*.

The distribution of the rust is interesting. In 1911 Johnson (19, p. 7) stated that it was common at least as far west as Minnesota and in 1914 Mercer (21, p. 20–22) recorded it as being common in North Dakota. In 1916 the writers found it very commonly in serious abundance in Minnesota, North Dakota, Montana, Idaho, Washington, Wyoming, Nebraska, Iowa, and Manitoba, Canada.

TABLE XXXIII.—*Results of inoculations with urediniospores of P. graminis agrostis*

Original host.	Immediate host.	Plant inoculated.	Trials. +	Trials. −	Result.	Degree of infection.
Agrostis alba	*Agrostis alba*	*Alopecurus geniculatus*	1	0	70/85	Heavy.
Do	do	*Alopecurus pratensis*	1	0	20/30	Moderate to heavy.
Do	do	*Anthoxanthum odoratum.*	0	1	0/35	
Do	do	*Avena sativa*	2	0	4/36	Weak.
Do	*Avena sativa*	do	0	1	0/11	
Agrostis stolonifera	do	do	1	1	2/22	Do.
Do	do	*Bromus inermis*	0	1	0/7	
Do	do	*Bromus tectorum*	1	0	24/24	Moderate.
Do	*Agrostis alba*	*Calamagrostis canadensis.*	1	0	3/45	Do.
Agrostis alba	do	*Dactylis glomerata*	1	0	16/16	Heavy.
Do	do	*Holcus lanatus*	1	0	35/45	Moderate.
Do	do	*Hordeum jubatum*	0	1	0/24	
Do	do	*Hordeum vulgare*	1	0	7/26	Weak.
Do	*Hordeum vulgare*	do	3	1	13/35	Do.
Do	*Agrostis alba*	*Koeleria cristata*	1	0	12/18	Moderate.
Do	do	*Phalaris canariensis*	0	2	0/17	
Do	*Avena sativa*	*Phleum pratense*	0	1	0/4	
Do	*Agrostis alba*	*Poa compressa*	0	1	0/18	
Do	do	*Secale cereale*	1	0	2/17	Weak.
Agrostis stolonifera	*Secale cereale*	do	0	1	0/4	
Do	*Agrostis stolonifera*	*Triticum vulgare*	0	1	0/34	
Do	*Agrostis canina*	do	0	1	0/19	
Agrostis alba	*Agrostis alba*	do	0	1	0/28	

Summary of results of inoculations with *P. graminis agrostis:*

Hosts found naturally infected: *Agrostis alba* L., *A. stolonifera* Vasey.

Easily infected by artificial inoculation: *Agrostis canina* L., *Alopecurus geniculatus* L., *A. pratensis* L., *Bromus tectorum* L., *Dactylis glomerata* L., *Holcus lanatus* L., *Koeleria cristata* (L.) Pers.

Weakly infected by artificial inoculation: *Avena sativa* L., *Calamagrostis canadensis* (Michx.) Beauv., *Hordeum vulgare* L., *Secale cereale* L.

Hosts not infected by artificial inoculation: *Anthoxanthum odoratum* L., *Bromus inermis* Leyss., *Hordeum jubatum* L., *Phalaris canariensis* L., *Triticum vulgare* Vill.

It seems probable that a number of species of Agrostis are hosts for *P. graminis agrostis*, although it was found in the field only on *A. alba* and *A. stolonifera*. The grasses which were easily infected artificially may harbor the rust in nature. It is quite possible that if more trials had been made *Calamagrostis canadensis* would also have proved more susceptible than it appeared to be, because the few leaves which became infected developed fairly normal uredinia. Of the three cereals, barley and oats are most easily infected. The uredinia are, however, always very small and few in number. It seems probable that *Phalaris canariensis*, *Hordeum jubatum*, and *Anthoxanthum odoratum* can be infected by the rust, although the inoculations made thus far have not resulted in successful infection. Negative results from a small number of trials often mean little.

Stuart, as reported by Arthur (7, p. 18), succeeded in infecting wheat with urediniospores from *Agrostis alba vulgaris*, but there is some possibility of error since the spores on wheat were larger than those from the original host. Carleton (7, p. 18) did not succeed in infecting wheat or oats with the rust from *Agrostis alba vulgaris*, and concludes that it is a distinct form. Eriksson gives *Agrostis alba* and *A. stolonifera* as hosts. Jaczewski (18, p. 353) gives *Agrostis alba* as host and states that the rust is also capable of infecting the following:

Secale cereale, Avena sativa, Triticum vulgare, Hordeum vulgare, Triticum repens, Dactylis glomerata, Bromus secalinus, Bromus inermis, Aira caespitosa, Apera Spica venti.

It is quite possible that the rust will be found in nature on a number of grasses. Although it probably occurs commonly in nature, it is doubtful if it is of practical importance on any of the cereals, since it can infect them only very weakly.

GENERAL DISCUSSION.

MORPHOLOGY OF UREDINIOSPORES [1]

In general the size and shape of urediniospores of different biologic forms of *Puccinia graminis* are similar. If, however, large numbers of spores are measured and the arithmetical mean or biometrical mode determined, it becomes quite apparent that there are appreciable and fairly constant differences, provided the spores measured be taken from congenial hosts. Jaczewski (18, p. 358) briefly summarizes the previous observations of similar nature, but states that he was unable to distinguish the different biologic forms in Russia by spores sizes. It can,

[1] Spore measurements were made by Mr. M. N. Levine. Only the dimensions of spores on congenial hosts are given; the other data will be presented in a separate paper.

however, be done if the spores of the various biologic forms are developed on congenial hosts under similar conditions and if enough spores are measured. The range of variability in size of urediniospores is sufficiently great to cause overlapping in some cases unless conditions have been uniform. A brief summary of the important characters of urediniospores of the different biologic forms is given. The sizes are given in Table XXXIV.

P. graminis tritici.—The spores are quite constant in size, shape and color. They are longer than those of any other forms, but in width they are about the same as those of *P. graminis avenae.* Shape is elliptic to ovate, color bright cadmium-yellow.

P. graminis tritici compacti.—Quite similar to *P. graminis tritici.* Color practically the same; spores slightly longer; shape, ovate to ellipsoid.

P. graminis secalis.—Uniform in size, shape and color. Shape elongate-elliptic; in length somewhat shorter than urediniospores of *P. graminis avenae,* in width approaching that of urediniospores of *P. graminis phleipratensis.* Color dull yellow to grayish, similar to that of *P. graminis phleipratensis.*

P. graminis avenae.—Color bright cadmium-yellow; size and shape very variable, shape ellipsoid, pyriform or globose.

P. graminis phleipratensis.—Shape mostly pyriform; color dull yellow to grayish; size fairly uniform.

P. graminis agrostis.—Spores very similar to those of *P. graminis phleipratensis,* possibly not quite so dominantly pyriform and somewhat smaller.

In order to facilitate ready comparison the spore dimensioms are grouped in Table XXXIV.

TABLE XXXIV.—*Comparative sizes in microns of urediniospores of biologic forms of Puccinia graminis*

Biologic form.	Size limits.	Modes.
P. graminis tritici (American form)	23. 04–40. 96×15. 04–24. 96	32. 64×19. 71
P. graminis tritici (Australian form)	25. 92–41. 60×16. 00–21. 76	33. 17×18. 66
P. graminis tritici compacti	24. 96–38. 08×14. 40–25. 28	31. 76×19. 52
P. graminis secalis	17. 92–38. 72×13. 44–21. 44	27. 23×16. 93
P. graminis avenae	19. 20–37. 12×13. 76–25. 60	28. 64×19. 49
P. graminis phleipratensis	16. 00–29. 76×12. 80–21. 12	23. 40×17. 31
P. graminis agrostis	17. 60–28. 48×13. 76–18. 88	22. 72×16. 16

It will be readily seen from Table XXXIV that there is considerable difference in the sizes of urediniospores of different biologic forms. Those of *P. graminis tritici* are largest and those of *P. graminis tritici compacti* differ only slightly. All the other forms are quite different, however, the spores of both *P. graminis avenae* and *P. graminis secalis* being shorter,

while those of the remaining two forms are very much smaller. The spores of the *avenae* and *secalis* forms do not differ greatly in length, but the spores of the form *avenae* are considerably thicker than those of the form *secalis*. The spores of the form *agrostis* are smaller than those of the form *phleipratensis*, especially in width.

APPEARANCE AND DEVELOPMENT OF UREDINIA

The general appearance of the uredinia of different biologic forms of stemrust on congenial hosts is, with minor exceptions, quite similar. The linear uredinia of *P. graminis phleipratensis* are, of course, distinctive, but even this character is not constant. The shape of uredinia on congenial hosts is usually oval or somewhat broadly linear, although, when heavy infection occurs, the uredinia may coalesce to such an extent that the identity of the individual uredinia is almost lost. The length varies from only 1 or 2 mm. to 0.5 cm. or more. The color is quite variable. Usually when the relative humidity is high or the light intensity low the color tends to become paler. On some hosts the epiderm is raised before the uredinia break out, giving the plant a blistered appearance in the infected area. The torn edges may persist for some time after the epiderm has been ruptured. Again, this appearance may be entirely absent.

The size, shape, and color of uredinia may vary greatly on semicongenial or uncongenial hosts. Very often the uredinia become rounder and very much smaller on such hosts. The color may also vary a great deal, so much, in fact, that it is sometimes necessary to transfer the rust back to the original host in order to become convinced that something has not gone wrong. Carleton (7, p. 16) long ago called attention to this fact, and it has been a matter of common observation since then. Of course, such differences are to be expected, just as one expects phanerogamic plants to vary with the conditions under which they are grown; but with the rusts this variation emphasizes the necessity of determining the performance before the identity can be established.

The incubation period of the various forms varies considerably on the same host. The age of the plant, the vegetative condition of the plant, the temperature, and the light intensity may affect the rate of development of the rust materially. The cereals are usually susceptible at any age up to ripening time. The susceptibility of some grasses, however, under greenhouse conditions at least, seems to vary more. No careful experiments were made to investigate this question thoroughly, but repeated observations were made under conditions which made accurate comparisons possible. Some plants, such as some species of Agropyron and Elymus, are extremely susceptible when young and much less so when older. In fact no infection, or at best very weak infection, occurred on some of these grasses when they were about 3 months old; while,

when they were only a week or two old, they became very heavily infected when inoculated with the same rust. Some of these same grasses, however, became infected under natural conditions in the field when quite old. Other grasses, such as *Phleum pratense* and *Agrostis alba*, seem to be more susceptible when they are older. It was often difficult to obtain normal infection on very young plants, while on older plants very heavy infection resulted from inoculations made under similar conditions. Other grasses again, such as *Dactylis glomerata*, seem equally susceptible at all ages. Whether these observations are of any significance can only be determined by carefully controlled experiments made on an extensive scale under varying conditions and with a large number of species of plants and different forms of rust. It seems quite possible that they may explain conflicting results obtained by the same investigators and possibly the discrepancies reported by different investigators. In fact, if the results of investigations by various workers are to be comparable, methods should be standardized with respect to kinds and ages of plants used as well as mechanical methods.

Temperature is important in determining the rate of development of the various biologic forms. No distinct differences were noted between the different forms; such differences, however, may have escaped observation. Contrary to a fairly general belief, stemrust seems to develop best at fairly high temperatures, provided conditions have been favorable for infection. The best infection usually results when the temperature is low enough to cause the condensation of moisture in a very fine film on the leaves. This usually occurs at night. Then, infection having taken place, the uredinia seem to develop more rapidly at higher temperatures up to a certain point, probably about 75° F. During extremely hot weather it is difficult to secure heavy infection, probably on account of the difficulty of inducing a film of water to form on the inoculated plants and on account of the effect of the heat on the vigor of the plants. Low temperatures, below about 65° F., also inhibit the development of the rust.

A considerable amount of sunlight is necessary for the best development of rust. Whether the effect is direct or indirect, the writers are unable to say. During periods of cloudy weather, however, the incubation period may be lengthened a week or more, and the rust does not develop so abundantly as during bright weather, as experiments to determine this showed. Plants were inoculated under the same conditions, placed under bell jars for the same length of time and kept side by side, except that some were partially shaded and the others kept in direct sunlight. The shaded plants invariably were more weakly infected than the others. Partially etiolated plants were infected with difficulty and the rust developed very weakly on them. No rust developed on etiolated plants. Careful and extensive experiments are desirable.

PARASITISM OF BIOLOGIC FORMS

The parasitism of some of the biologic forms is surprisingly similar. Often the reaction of only one or two host plants distinguishes one form from another. By reference to Tables XXVIII to XXXIII it is quite apparent that *P. graminis tritici*, *P. graminis tritici compacti*, and *P. graminis secalis* fall naturally into one group, so far as parasitism is concerned. In the same way *P. graminis avenae*, *P. graminis agrostis*, and *P. graminis phleipratensis* fall into another.

There are a number of common hosts for *P. graminis tritici*, *P. graminis tritici compacti*, and *P. graminis secalis*. From the results thus far obtained it is very evident that a number of species of the genera Agropyron, Elymus, and Hordeum are about equally congenial hosts for these three biologic forms. The first two can be distinguished from each other definitely, so far as present knowledge goes, only by their action on *Triticum vulgare*, while *P. graminis secalis* differs from both in its effect on *Secale cereale* and *Agropyron repens*. These differences are, however, very distinct and apparently quite constant. The matter of the constancy of the forms will be dealt with fully in a subsequent paper.

P. graminis avenae, *P. graminis agrostis*, and *P. phleipratensis* are also similar parasitically. *Koeleria cristata*, *Holcus lanatus*, *Alopecurus pratensis*, *A. geniculatus*, and *Dactylis glomerata* are common hosts for all three. *P. graminis agrostis* and *P. phleipratensis* attack *Avena sativa* in about the same degree. The infection is always weak, the uredinia nearly always being very minute. *Hordeum vulgare* and *Secale cereale* are infected weakly by all three. Exhaustive experiments on these three forms are very desirable and may yield interesting results.

All of the biologic forms studied can develop, at least to a limited extent, on *Hordeum vulgare*, *Secale cereale*, and possibly on other hosts. The degree of infection varies widely, however, as previously noted.

RELATION OF WILD GRASSES TO RUST EPIDEMICS

From a practical standpoint the effect of the wild grasses on cereal-rust epidemics is important. The influence of the grasses would seem to be possibly significant in three ways: (1) In permitting the overwintering of the rust in the mycelial or urediniospore stage, (2) in aiding in the dissemination of rust, and (3) in possibly breaking down the specialization of the biologic forms in nature.

The writers have done preliminary work on the overwintering of rust on wild grasses, but are not prepared to draw definite conclusions. Certainly urediniospores of *P. graminis phleipratensis* can survive the winter in some localities. Johnson (19, p. 12–13) showed this to be true at Arlington, Va., and Hungerford (17) showed the same to be true in Wisconsin. Mercer (21) states that in North Dakota urediniospores of timothy rust are hard to find after the first hard freeze. Observations

made by the writers at St. Paul, Minn., in the winter of 1916–17, an unusually severe one, indicate quite clearly that the urediniospores survive the winter quite easily in Minnesota. A summary of the experiments made on the overwintering of various cereal rusts is given by Freeman and Johnson (14, p. 45–53), who also found that *P. graminis* and probably *P. rubigo-vera* could survive the winter in the uredinial stage at St. Paul, Minn. Bolley and Pritchard (4, p. 642) had previously shown this to be true for *P. rubigo-vera* in a number of regions. From preliminary observations it seems quite probable that urediniospores of *P. graminis* are injured by heat and drying more than by low temperatures. If this is true, the extent to which the rust overwinters may depend on the amount of rain in the fall and on the amount of snow in the winter. It would be very interesting to make extensive observations in regions of high altitude, where snow comes early. Abundant urediniospores occur on various grasses in the fall when the snows begin, and it is possible that in such regions overwintering is very common. Further investigations are needed.

There can be little question that grasses aid very materially in the dissemination of rust. Enormous numbers of urediniospores are developed on grasses, and these are undoubtedly blown long distances by the wind. Whether the grasses are important in initiating the early spring infections, however, is another matter. If the uredinial stage of the rust persists on grasses throughout the winter, they probably are responsible for much of the early infection. Even if such overwintering is of infrequent occurrence, however, grasses may still be important because they usually are nearer barberries than grain fields are. They may become infected, develop urediniospores in a week or 10 days, and these may then blow to other grasses or cereals and thus spread during the entire growing season.

An excellent summary of observations on the effect of barberry on surrounding cereals and grasses is given by Freeman and Johnson (14, p. 28–45) and by Pritchard (22, p. 169–175) and need not be repeated here. Pritchard (22, p. 179–181), as a result of experiments in North Dakota, concludes that barberry plants have but little effect in starting rust epidemics in the spring, because—

> *P. graminis* probably appeared upon the experimental plot of winter wheat almost or quite as early as upon *Agropyron repens* and *Hordeum jubatum* even when the latter were in the immediate vicinity of the barberry. * * * With the exception of the one case mentioned under date of June 27, the uredospores of *P. graminis* were generally present upon the spring wheat earlier than they were observed upon the wild grasses remote from the barberry bushes.

He states further—

> that one form of *P. graminis* is common to *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, *Avena fatua*, oats, and rye, but is incapable of infecting either barley or wheat. This furnishes little encouragement to those who believe that *P. graminis*

is spread to the wheat fields from the barberry bushes or from occasional protected spots, as beneath ice, by the aid of the native grasses.

The experience of the writers does not agree entirely with that of Pritchard. As mentioned previously, the writers are in doubt as to the importance of the overwintering of the uredinial stage on grasses. But observations made in Minnesota for the past few years indicate that barberries may be important, at least locally.

In 1914 numerous well-developed æcia of *P. graminis secalis* were found on barberry growing near Lake Minnetonka, Minn., as early as May 17. Successful infection was repeatedly obtained on rye and barley, but not on wheat or oats. At this time there was no rust on barley or rye in the region, but *Agropyron repens* near the barberries soon became heavily rusted. New æcia continued to be developed at irregular intervals until July 10 and possibly longer. Pycnia began to appear on barberries on University Farm, St. Paul, on May 18 and by May 22 æcia had formed. Wheat, oats, barley, and rye were inoculated with the æciospores on May 23, and wheat and barley became infected, while oats and rye did not, showing that the rust was *P. graminis tritici*. Æcia developed in great abundance on another group of barberries on University Farm about May 20. By June 9 volunteer rye, *Agropyron repens*, and *Hordeum jubatum* near these barberries had become very severely rusted. Inoculations made with both æciospores and the urediniospores showed that both *P. graminis secalis* and *P. graminis tritici* were present. Most of the rust was *P. graminis secalis*. At this time grasses and wheat at some distance from the barberries were not at all rusted. Winter wheat near barberries was beginning to rust.

In 1915 viable æciospores were obtained at University Farm on May 8. These proved to be *P. graminis tritici*. Successive crops of æcia were produced until about July 1, and, as in the previous year, both near these barberries and others bearing æcia of *P. graminis secalis*, grasses and cereals, when these were growing near, rusted severely while those at some distance remained free for about a month, when the rust began to appear quite generally on grasses. On July 10, at Dickinson, N. Dak., *Agropyron repens*, *A. tenerum*, and *Hordeum jubatum* were found very badly rusted near a group of barberries, while the same grasses and wheat half a mile away were just beginning to rust. On July 12, at Jamestown, N. Dak., *Hordeum jubatum* was found badly rusted near a field of Marquis wheat which was just beginning to rust slightly. A few miles away *A. smithii* was literally covered with urediniospores; in fact, the ground was red with them, and a field of wheat next to the grass was just beginning to rust. No barberries were seen, because lack of time prevented a search on farmsteads near by. The observations merely emphasize the fact that grasses do sometimes rust before cereals, and that the rust may spread from them to the cereals.

Æcia did not appear on barberries as early in 1916 as in 1915, owing probably to the late spring. Very heavy infection of barberries with *P. graminis secalis* was observed in Hennepin County, Minn., on May 26, and a few days later æcia of *P. graminis tritici* were found. By June 15 æcia were abundant in many localities. New æcia continued to be developed until well into July. The unusual number of æcia was very noticeable. Barberry bushes were often rendered unsightly on account of the severity of rust attack. By July 5 rust was becoming fairly abundant on many grasses, and a number of cases were observed where various grasses were severely affected, while wheat, barley, and rye near by were just beginning to develop a moderate amount of rust. This was especially true of *Hordeum jubatum*, which, on account of its habit of growth, furnishes very favorable conditions for infection.

The above observations show that grasses, at least in Minnesota, often become severly rusted near barberries in the spring or early summer before rust is present to any extent elsewhere. It seems quite probable that the urediniospores may be blown considerable distances by the wind and may infect other grasses and cereals. While the writers do not wish to be understood as maintaining that the sequence of barberry to grass to cereal is responsible for general rust attacks, it is not at all improbable that locally this may be very important. While it is true that the percentage of viable æciospores is often low, nevertheless sufficient numbers germinate to cause heavy epidemics on grasses early in the season. The possibility of transfer from the grasses or from the barberries directly to cereals depends, of course, on the biologic form present. *P. graminis tritici* and *P. graminis secalis* are often found on the same barberries; and *P. graminis avenae* is not uncommon. Fortunately this phase of the rust problem is being attacked vigorously by the Office of Cereal Investigations, United States Department of Agriculture.

SUMMARY

(1) *Puccinia graminis* has been collected on about 35 species of grasses in the upper Mississippi Valley, a part of the Northern Great Plains region, and a small area of the Pacific Northwest.

(2) Inoculation experiments with the rust from about 30 grasses were made and the following biologic forms were isolated: *Puccinia graminis tritici, P. graminis tritici compacti, P. graminis secalis, P. graminis avenae, P. graminis phleipratensis,* and *P. graminis agrostis.*

(3) *P. graminis tritici compacti* was found only in the Palouse country of Washington and Idaho; it occurs on club wheat and grasses which, east of the Rocky Mountains, are hosts for *P. graminis tritici.* No ordinary *P. graminis tritici* was found west of the Rocky Mountains.

(4) More than one biologic form may occur on the same host in nature, sometimes even on the same plant. In such cases it is necessary to

employ differential hosts to determine the identity of the forms. *P. graminis tritici* and *P. graminis secalis* have been found associated most often.

(5) Different strains of the same bioligic form sometimes differ in virulence on the same hosts; but the differences are usually in degree only.

(6) There seems to be no sharp geographical specialization of biologic forms in the upper Mississippi Valley and Northern Great Plains area, where the biologic forms are quite uniform.

(7) On the basis of parasitism the biologic forms can be divided into two groups: (1) *P. graminis tritici*, *P. graminis tritici compacti*, and *P. graminis secalis;* (2) *P. graminis avenae*, *P. graminis phleipratensis*, and *P. graminis agrostis.*

(8) Wheat, club wheat, rye, and *Agropyron repens* are differential hosts for group 1. The *tritici* form infects wheat and club wheat readily and rye and *A. repens* weakly; the *tritici compacti* form attacks club wheat readily and the other three weakly; the *secalis* form develops normally on rye and *A. repens*, but very rarely attacks the other two. All three develop well on barley, *Hystrix patula*, and *Bromus tectorum* and on a number of species of Agropyron, Elymus and Hordeum.

(9) Differential hosts for the forms in group 2 are oats, *Phleum pratense*, and *Agrostis* spp. The *avenae* form develops normally on oats, infects *Phleum pratense* weakly, and develops fairly well on *Agrotis alba;* the *phleipratensis* form grows normally on *Phleum pratense*, infects oats rather weakly, and has not yet infected *Agrostis alba;* the *agrostis* form develops normally on *Agrostis* spp., infects oats very weakly, and has not yet infected *Phleum pratense.* All three infect barley and rye weakly, but develop well on *Koeleria cristata*, *Holcus lanatus*, *Dactylis glomerata*, *Alopecuris geniculatus*, and *A. pratensis.*

(10) Barley, rye, and *Bromus tectorum* have been infected by all six biologic forms. Oats have been infected by all but *P. graminis tritici compacti*, but not enough trials have been made with this form.

(11) All gradations in susceptibility occur, from complete immunity to complete susceptibility to various biologic forms. The following reactions may be made to inoculation: No visible effect; appearance of small flecks; production of very minute uredinia without any flecks; production of minute uredinia in either small or large dead areas; development of moderately large uredinia in small, medium, or large flecks; production of large uredinia surrounded by small dead areas or by apparently healthy tissue.

(12) The biologic forms can be distinguished from each other morphologically as well as parasitically. The size, shape, and color of the urediniospores are the distinguishing characters. The determination of biometrical modes permits identification with a reasonable degree of cer-

tainty if the spores measured have been developed under approximately similar conditions.

(13) The rate of development of a given biologic form depends on the vigor of the rust strain, the kind, and sometimes the age of the host plant, the amount of light, heat, and humidity. Sunlight, high relative humidity, and moderate temperatures, up to about 75° F., are favorable to rust development.

(14) Preliminary observations were made on the overwintering of the uredinial stage on grass hosts, but definite conclusions have not been reached, except for *P. graminis phleipratensis* which survived the very severe winter of 1916–17 at St. Paul, Minn., very easily.

15) There is evidence to show that grasses often rust in the spring or early summer before rust appears in grain fields in the same vicinity. This is especially true if grasses are near barberries. The rust thus developed early in the season has usually been the rye and wheat stemrust forms.

(16) Inconceivably large numbers of urediniospores are produced by various grasses in cereal-growing regions. Unquestionably, therefore, grasses are very important in increasing the amount of infective material and in this way, if in no other, they are important in the cereal-rust problem.

LITERATURE CITED

(1) ARTHUR, J. C.
1905–08. CULTURES OF UREDINEAE IN 1904–07. *In* Jour. Mycol., v. 11, no. 76, p. 50–67, 1905; v. 12, no. 81, p. 11–27, 1906; v. 13, no. 91, p. 189–205, 1907; v. 14, no. 93, p. 7–26, 1908.

(2) ———
1909–10. CULTURES OF UREDINEAE IN 1908–09. *In* Mycologia, v. 1, no. 6, p. 225–256, 1909; v. 2, no. 5, p. 213–240, 1910.

(3) BOLLEY, H. L.
1891. WHEAT RUST: IS THE INFECTION LOCAL OR GENERAL IN ORIGIN? *In* Agr. Sci., v. 5, no. 11/12, p. 259–264.

(4) ——— and PRITCHARD, F. J.
1906. RUST PROBLEMS. FACTS, OBSERVATIONS AND THEORIES. POSSIBLE MEANS OF CONTROL. N. Dak. Agr. Exp. Sta. Bul. 68, p. 607–672, 30 fig.

(5) CARLETON, M. A.
1893. NOTES ON THE OCCURRENCE AND DISTRIBUTION OF UREDINEÆ. *In* Science, v. 22, no. 548, p. 62–63.

(6) ———
1899. CEREAL RUSTS OF THE UNITED STATES: A PHYSIOLOGICAL INVESTIGATION. U. S. Dept. Agr. Div. Veg. Phys. and Path. Bul. 16, 74 p., 1 fig., 4 col. pl. Bibliography, p. 70–73.

(7) ———
1904. INVESTIGATIONS OF RUSTS. U. S. Dept. Agr. Bur. Plant. Indus. Bul. 63, 29 p., 2 col. pl.
Refers to statement by Arthur, p. 18, footnote.

(8) ERIKSSON, Jakob
1894. UEBER DIE SPECIALISIRUNG DES PARASITISMUS BEI DEN GETREIDEROST-PILZEN. *In* Ber. Deut. Bot. Gesell., Bd. 12, Heft 9, p. 292–331. Literatur-verzeichniss, p. 330–331.

(9) 1896. WELCHE GRASARTEN KÖNNEN DIE BERBERITZE MIT ROST ANSTECKEN? *In* Ztschr. Pflanzenkrank., Bd. 6, Heft 4, p. 193–197.

(10) ERIKSSON, Jakob.
1897. WEITERE BEOBACHTUNGEN ÜBER DIE SPEZIALISIERUNG DES GETREIDESCHWARZROSTES. *In* Ztschr. Pflanzenkrank., Bd. 7, Heft 4, p. 198–202.

(11) ———
1902. UEBER DIE SPEZIALISIERUNG DES GETREIDESCHWARZROSTES IN SCHWEDEN UND IN ANDEREN LÄNDERN. *In* Centbl. Bakt. [etc.], Abt. 2, Bd. 9, no. 16, p. 590–607; no. 17/18, p. 654–658.

(12) ——— and HENNING, Ernst.
1894. DIE HAUPTRESULTATE EINER NEUEN UNTERSUCHUNG ÜBER DIE GETREIDEROSTE. *In* Ztschr. Pflanzenkrank., Bd. 4, 66–73; 140–142, 197–203, 257–262.

(13) ——— ———
[1896.] DIE GETREIDEROSTE. . . . 463 p., 5 fig., 13 col. pl. Stockholm. Literaturverzeichnis, p. 446–457.

(14) FREEMAN, E. M., and JOHNSON, E. C.
1911. THE RUSTS OF GRAINS IN THE UNITED STATES. U. S. Dept. Agr. Bur. Plant Indus. Bul. 216, 87 p., 2 fig., 1 pl. Biboligraphy, p. 79–82.
Refers to statement by Derr (p. 18, footnote.)

(15) HITCHCOCK, A. S., and CARLETON, M. A.
1893. PRELIMINARY REPORT ON RUSTS OF GRAIN. Kans. Agr. Exp. Sta. Bul. 38, 14 p., 3 pl.

(16) ——— ———
1894. SECOND REPORT ON RUSTS OF GRAIN. Kans. Agr. Exp. Sta. Bul. 46, 9 p.

(17) HUNGERFORD, C. W.
1914. WINTERING OF TIMOTHY RUST IN WISCONSIN. *In* Phytopathology, v. 4, no. 4, p. 337–338.

(18) JACZEWSKI, A. A.
1910. STUDIEN ÜBER DAS VERHALTEN DES SCHWARZROSTES DES GETREIDES IN RUSSLAND. *In* Ztschr. Pflanzenkr., Bd. 20, Heft 6, p. 321–359, 8 fig.

(19) JOHNSON, E. C.
1911. TIMOTHY RUST IN THE UNITED STATES. U. S. Dept. Agr. Bur. Plant Indus. Bul. 224, 20 p.

(20) KLEBAHN, Heinrich.
1904. DIE WIRTWECHSELNDEN ROSTPILZE. . . . 447 p., illus., 6 pl. Berlin. Literatur, p. ix–xxxvii.

(21) MERCER, W. H.
1914. INVESTIGATIONS OF TIMOTHY RUST IN NORTH DAKOTA DURING 1913. *In* Phytopathology, v. 4, no. 1, p. 20–22.

(22) PRITCHARD, F. J.
1911. A PRELIMINARY REPORT ON THE YEARLY ORIGIN AND DISSEMINATION OF PUCCINIA GRAMINIS. *In* Bot. Gaz., v. 52, no. 3, p. 169–192, pl. 4. Literature cited, p. 190–192.

(23) ———
1911. THE WINTERING OF PUCCINIA GRAMINIS TRITICI E. & H. AND THE INFECTION OF WHEAT THROUGH THE SEED. *In* Phytopathology, v. 1, no. 5, p. 150–154, 2 fig., pl. 22.

(24) STAKMAN, E. C.
1914. A PRELIMINARY REPORT ON THE RELATION OF GRASS RUSTS TO THE CEREAL RUST PROBLEM. (Abstract.) *In* Phytopathology, v. 4, no. 6, p. 411.

(25) STAKMAN, E. C.
1914. A STUDY IN CEREAL RUSTS: PHYSIOLOGICAL RACES. Minn. Agr. Exp. Sta. Bul. 138, 56 p., 9 pl. Bibliography, p. 50–54.

(26) ——— and JENSEN, Louise.
1915. INFECTION EXPERIMENTS WITH TIMOTHY RUST. *In* Jour. Agr. Research, v. 5, no. 5, p. 211–216. Literature cited, p. 216.

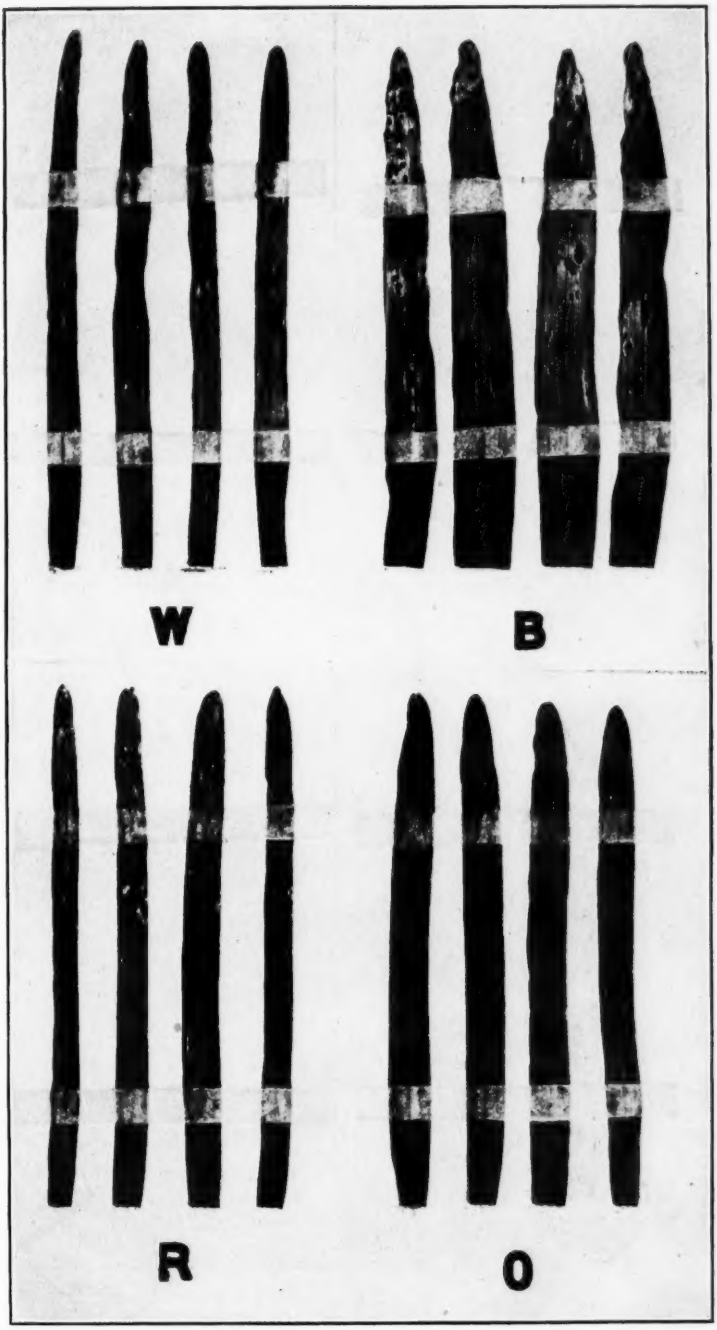
(27) ——— and PIEMEISEL, F. J.
1916. BIOLOGIC FORMS OF PUCCINIA GRAMINIS ON WILD GRASSES AND CEREALS. A PRELIMINARY REPORT. (Abstract.) *In* Phytopathology, v. 6, no. 1, p. 99–100.

(28) ——— ———
1916. INFECTION OF TIMOTHY BY PUCCINIA GRAMINIS. *In* Jour. Agr. Research, v. 6, no 21, p. 813–816. Literature cited, p. 816.

(29) ——— ———
1917. A NEW STRAIN OF PUCCINIA GRAMINIS. (Abstract.) *In* Phytopathology, v. 7, no. 1, p. 73.

PLATE 53

Puccinia graminis tritici on wheat (*W*), barley (*B*), rye (*R*) and oats (*O*) 11 days after inoculation. Normal uredinia on wheat and barley; small uredinia and sharp flecks on rye; no infection on oats.


W
B
R
O

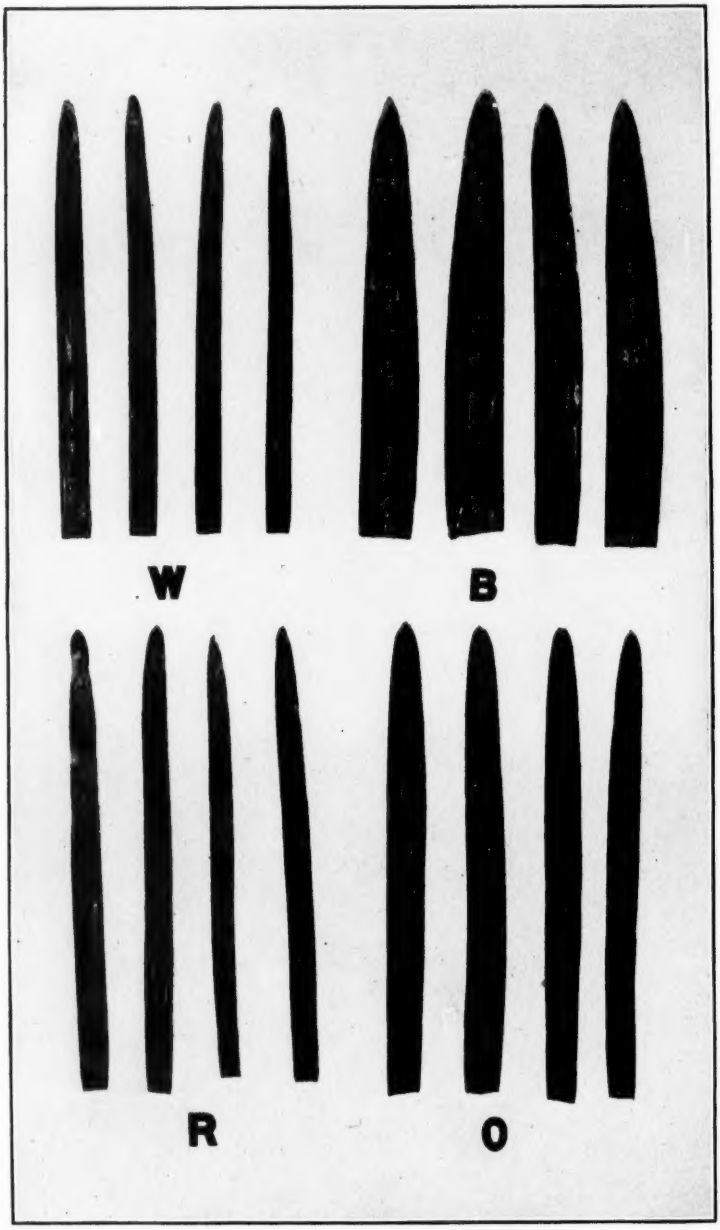

W
B
R
O

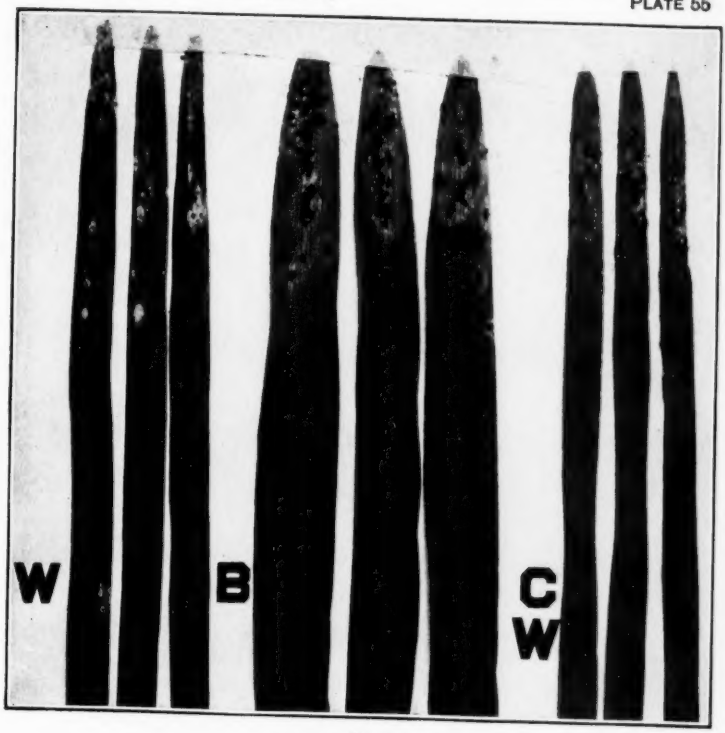
PLATE 54

Puccinia graminis tritici compacti on wheat (*W*), barley (*B*), rye (*R*), and oats (*O*) 10 days after inoculation. Very small uredinia in sharp dead areas on wheat; normal development on barley; small uredinia and distinct flecks on rye; no infection on oats.

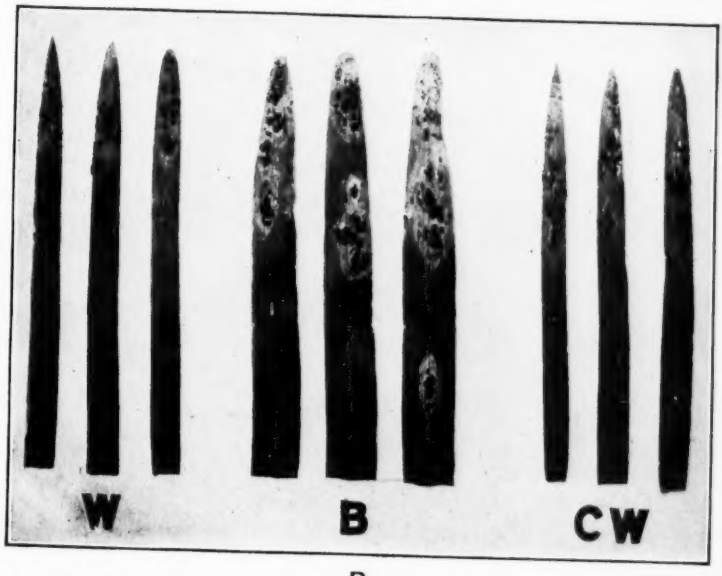
PLATE 55

A.—*Puccinia graminis tritici compacti* on *Triticum vulgare* (*W*), barley (*B*), and *Triticum compactum* (*CW*)—that is on common wheat, barley, and club wheat. Normal development on barley and club wheat, common wheat showing minute uredinia and hypersensitiveness as indicated by sharp flecks. Compare with figure B.

B.—*Puccinia graminis tritici* on *Triticum vulgare* (*W*), barley (*B*), and *Triticum compactum* (*CW*)—that is, on common wheat, barley, and club wheat. Normal development on all three cereals. Compare with figure A.



A



B

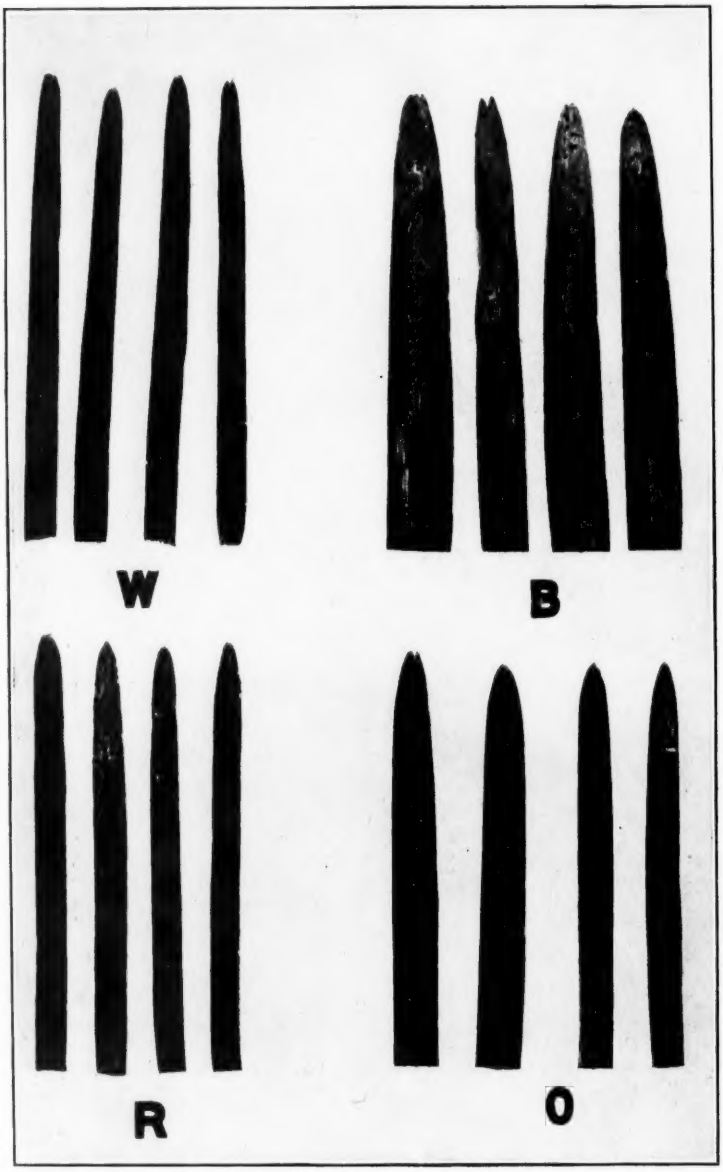
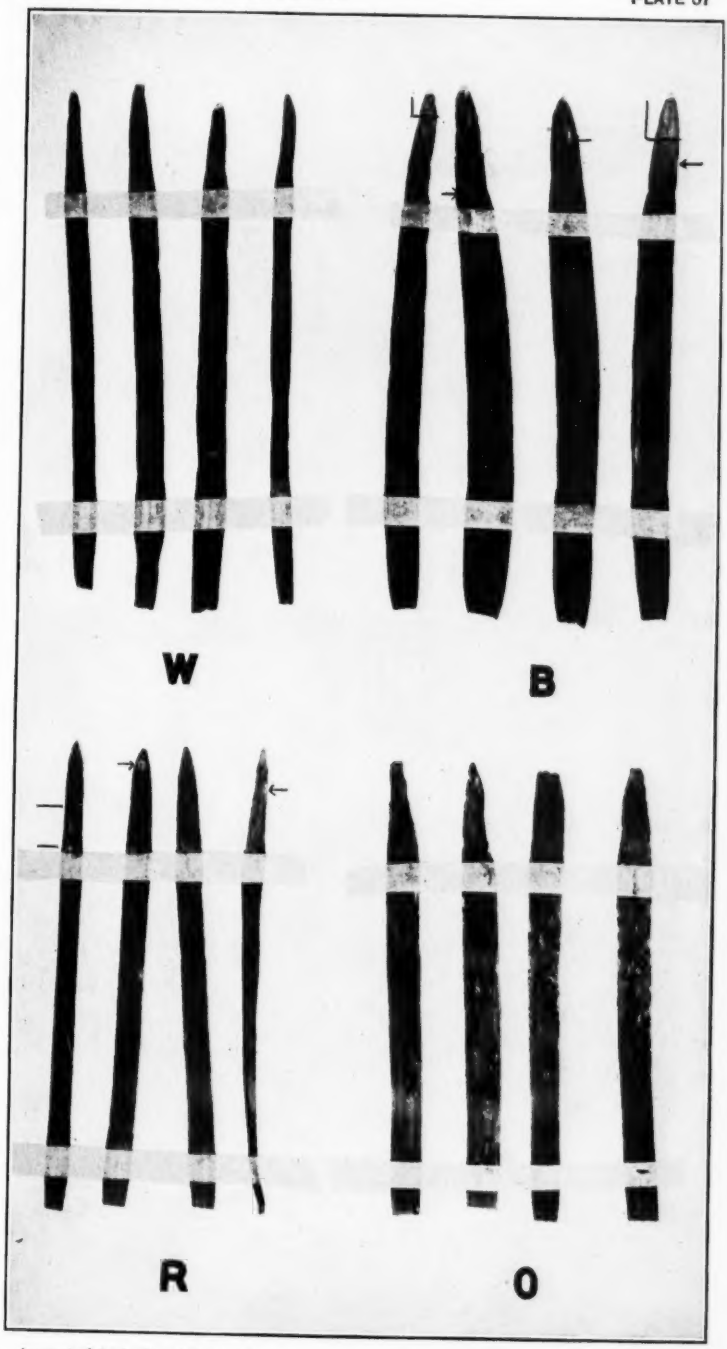

W
B
R
O

PLATE 56

Puccinia graminis secalis on wheat (*W*), barley (*B*), rye (*R*), and oats (*O*). Normal but rather weak development on barley and rye. No infection on oats and wheat. (Very small uredinia are rarely produced on wheat and oats.) Twelve days after inoculation.

PLATE 57

Puccinia graminis avenae on wheat (*W*), barley (*B*), rye (*R*), and oats (*O*). Normal development on oats; small uredinia in very small, dead areas on barley and rye (location of single uredinia indicated by arrows; groups between lines); no infection on wheat. Ten days after inoculation.


W
B
R
O

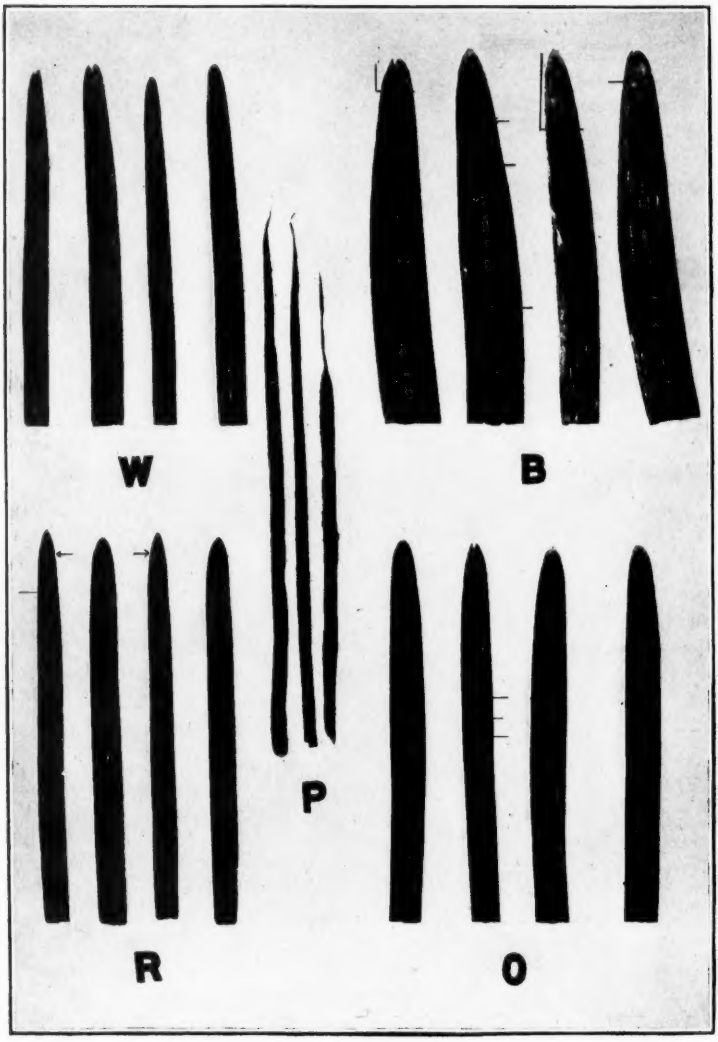
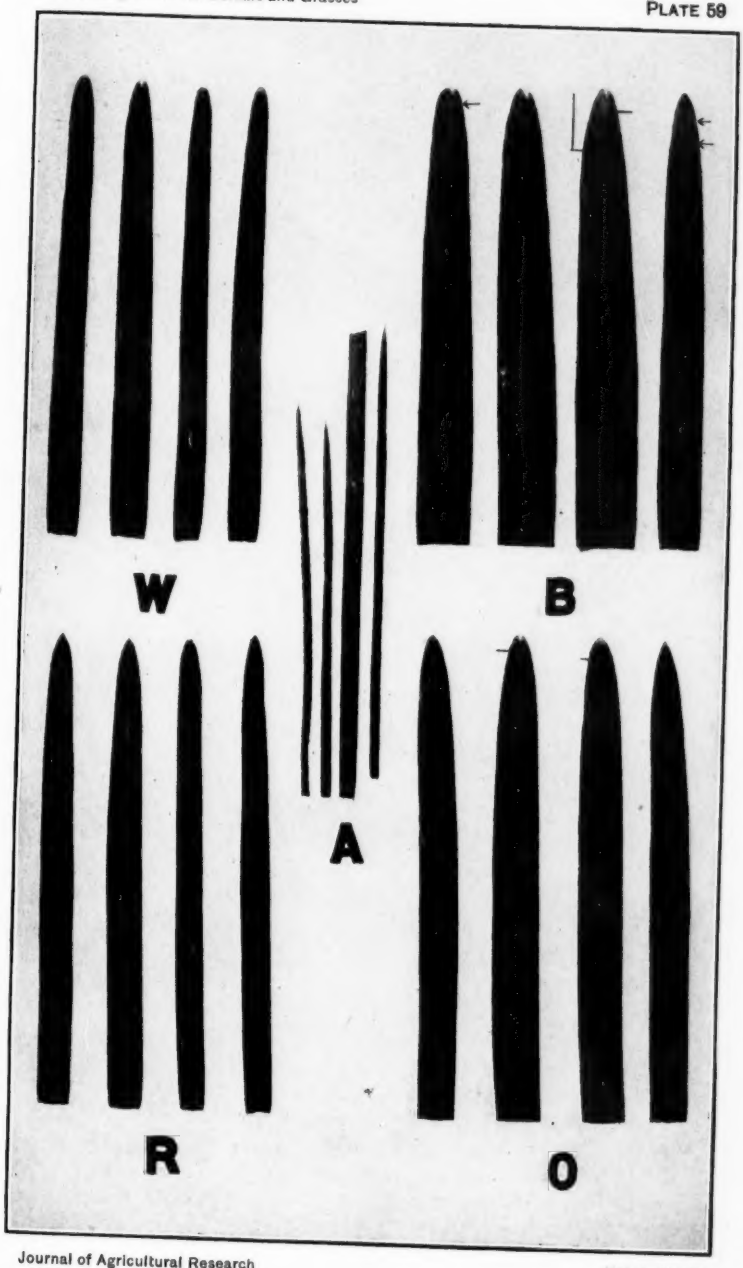

W
B
P
R
O

PLATE 58

Puccinia graminis phleipratensis on wheat (*W*), barley (*B*), rye (*R*), oats (*O*), and *Phleum pratense* (*P*). Normal development on *Phleum;* small uredinia on barley, rye, and oats (location shown by arrows or lines); some flecks without uredinia on barley and rye; no infection on wheat. Fourteen days after inoculation.

PLATE 59

Puccinia graminis agrostis on wheat (*W*), barley (*B*), rye (*R*), oats (*O*), and *Agrostis alba* (*A*). Minute uredinia on barley and oats; normal infection on *Agrostis alba;* no infection on wheat or rye (rye is sometimes weakly infected).


W
B
A
R
O